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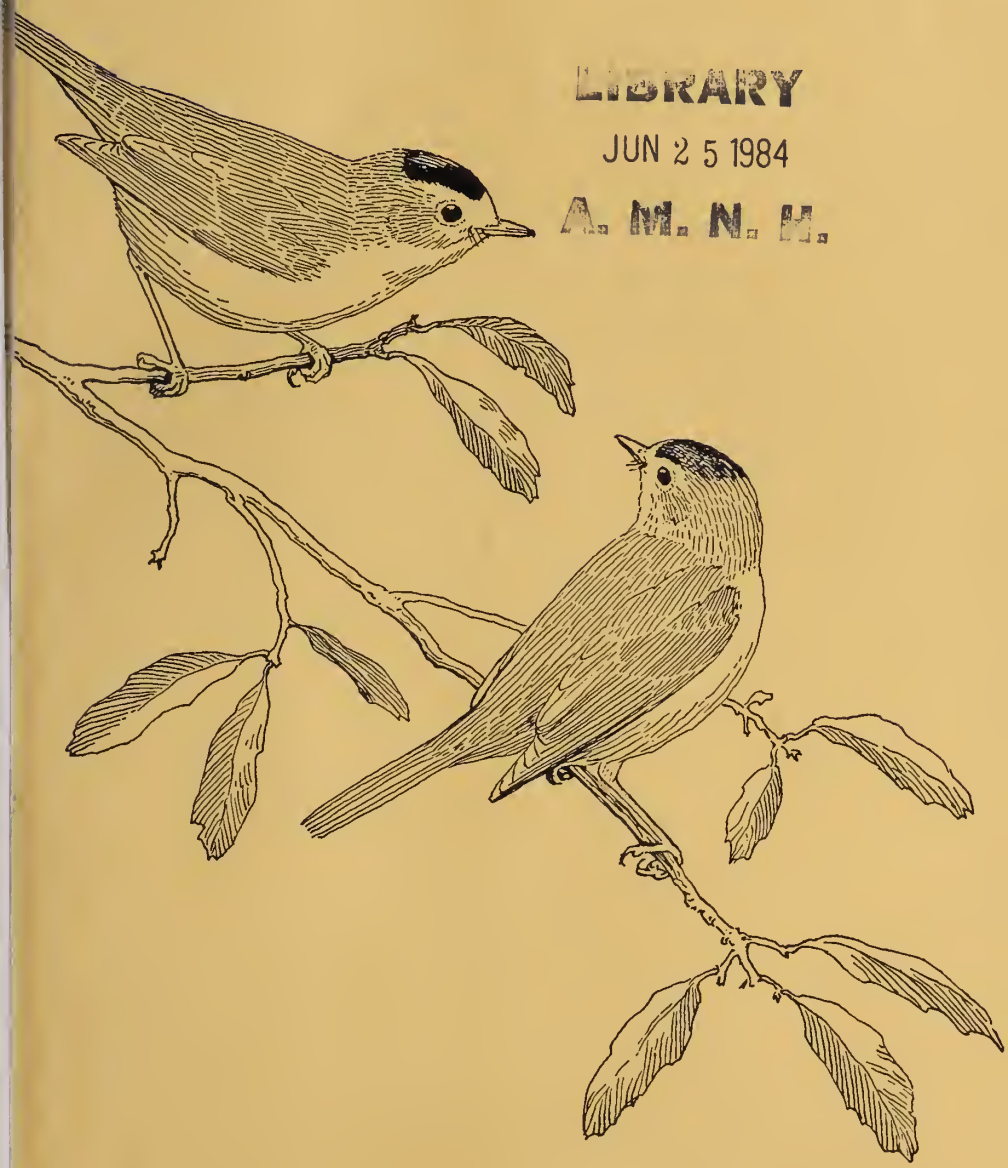

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Guiana Crested Eagles *(Morphnus guianensis):*
male (pale bird – left) and female (dark bird – right) at the nest.
Photograph by Richard O. Bierregaard, Jr.

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OBSERVATIONS OF THE NESTING BIOLOGY OF THE GUIANA CRESTED EAGLE (*MORPHNUS GUIANENSIS*)

RICHARD O. BIERREGAARD, JR.

The natural history of the Guiana Crested Eagle (*Morphnus guianensis*) is poorly known (Wetmore 1965). Most information currently available is based on casual observations; for examples see Wetmore (1965) or Lehmann (1943). Here I present the first detailed observations of the nesting of one of the largest forest dwelling raptors in the Americas.

Morphnus guianensis occurs from Honduras to northern Paraguay and Argentina, where it is restricted to lowland tropical forests (Brown and Amadon 1968). Lehmann (1943) reports that it is encountered exclusively in the wettest, warmest areas of dense forest along the coast or at river edges.

Discovery of the nest.—On 6 March 1980 a male *M. guianensis* was spotted moving through the canopy and subsequently followed to a nest. The nest was about 28 m above the ground in the first fork of a large Lecythidaceae (common name = jararana). The tree was not an emergent, but due to the local terrain, afforded a view of about 70 m of the canopy east of the nest. The nest was located in virgin forest 80 km north of Manaus, Brasil (2°25′S × 59°50′W), approximately 20 km from the Río Urubu, the closest river. Soils in the region are predominantly nutrient-poor yellow, alic latosols of high clay content on which the forest canopy reaches about 37 m. Emergents can be as tall as 45 m. The canopy is fairly regular in contour and closed, letting little light onto the forest floor. The understory is fairly open, typically with many stemless palms. The terrain has significant microrelief due to the many streams that intersect the forest. Annual rainfall over the last 30 years in nearby Manaus has averaged 2186 mm, falling mostly during December through April (Anonymous 1978).

Observations at the nest: pre-egg-laying.—A vocalization heard at the

time of discovery, from either the male or female, was a shrill, high pitched whistle, reminiscent of a bosun's whistle, *youuu-ree,* the final note short and ascending.

At dawn (06:00) on 7 March, the light-phase male landed in the nest and copulated with the female, an extreme dark-phase bird, which had been in the nest in an incubating posture. Copulation was brief (shorter than 10 sec) after which the male hopped from perch to perch near the nest, aware of my presence but, judging by his relaxed posture and the lack of attention paid to an observer directly beneath him, apparently unperturbed. His call during this time was a single high-pitched whistle.

The differences between the birds made it apparent why the relatively rare (Wetmore 1965, Blake 1977) dark phase was once considered a separate species, *M. taeniatus* Gurney (1879) (see Frontispiece). The female, with a slate black head, neck, and upper chest, and heavy black barring on the lower chest and underwings, was strikingly different from the pale male, with white ventral plumage finely barred with orange brown below the pale grey head, neck, and breast. The grey scalloping on the male's upperwing coverts in contrast to the female's solid dark upper surface, without the white and grey tips to the wing coverts mentioned by Wetmore (1965), further accentuated the difference between the pair.

Eggs, and incubating behavior.—On 10 April I climbed a tree adjacent to the nest tree and found two large creamy-colored eggs in the nest depression. Brown and Amadon (1968) refer to one set of eggs, purportedly of this species, which were cream-colored with large pale yellow-brown spots at the broad end and finer spots over the rest of the surface. The female, who remained within about 20 m of the nest, was not aggressive as I climbed above the nest about 5 m from the nest tree. During my descent, she returned to the nest. This docile behavior is similar to that reported by Rettig (1978) for a pair of Harpy Eagles (*Harpia harpyja*) in similar circumstances in Surinam. I never climbed the nest tree.

Young in the nest.—On 1 May I began to construct a nest-level blind in a tree 10 m from the nest. At this time, only one young was evident and appeared to be no more than a few days old. Working 1 h or so a day, the blind was completed by 6 May at which time observations of the nest commenced.

From 6 May–8 June, 70 h were spent in the blind on 13 separate days. During the month of observation, the female was in almost constant attendance at the nest. Upon my arrival at the blind (usually at about 06:00) she would flush from the nest, but return quickly, often within a minute of my disappearing into the blind. When I descended from the blind, the female remained in the nest and watched as I disappeared into the vegetation below the blind and nest.

During the first 2 weeks of observation, the female spent most of her time in a brooding position, although not always actually on the young. During very sunny days she stood above the young with wings slightly extended to shade it, while on rainy days she assumed a brooding posture and pulled the young to her chest.

The female was meticulous about the nest. Almost every time she returned to the nest without food, she brought a fresh bough torn off the nest tree or one nearby. When she alighted in the nest, often with the bough in her beak, she pulled individual leaves off the bough and put them around the rim of the nest. The female was fastidious about intestines and stomachs of prey items which she carried from the nest in her beak immediately after feeding. At the conclusion of the study no prey remains were discovered beneath the nest.

During the first 3 weeks of observation, or until the young was about 4 weeks old, the male appeared to be the sole provider for the three birds, as the female never strayed from the nest for more than 30 min, and could usually be heard moving about in the canopy during this time. When delivering food, the male announced his arrival in the nest area with a repeated, single note high-pitched call to which the female responded with a two syllable loud and high pitched, shrill *wee hee.* When the female heard the male's approach call, she immediately mantled over any prey remaining in the nest, her extended wings pumping with each syllable of her answering call. When the male landed in the nest to deliver prey items the female quickly snatched the food from him and mantled over the newly delivered item, as Rettig (1978) reported for the Harpy Eagle. The male usually remained in the nest less than 1 min.

Nest failure.—On 14 June the nest was empty, with no sign of the young either in the nest or on the ground below. The young had appeared healthy on the previous visit and the female was present and delivering food to the nest. Possible explanations for the failure of the nest include the death of one or both of the adults, most likely at the hands of a hunter from a nearby ranch, or the loss of the young while the female was away from the nest to a predator such as a tayra (*Eira barbara*), a large arboreal mustelid occasionally seen moving through the canopy, or another large raptor.

Feeding behavior.—Including prey items present in the nest at the beginning of a day's observation, 15 items were seen. These include six snakes (one rainbow boa, [*Eunectes murinus*], three emerald tree boas, [*Corallus caninus*], and two unidentified snakes, one of which may well have been a rainbow boa), one unidentified frog, perhaps *Phylomedusa bicolor,* and eight mammals. The mammals were small; estimated from the usually headless prey items that the male delivered, total body length

was about 20–35 cm, excluding tails. I believe most were probably either cricetine or hystricomorph rodents or marsupials. Although squirrels (*Sciurus gilvigularisi*) are the most conspicuous small to medium sized mammal in the area, none were observed as prey items in this nest. On the last day of observation, a kinkajou (*Potus flauvus*) was delivered to the nest by one of the parents. At 10:10 the female left the nest and returned 30 min later with a second kinkajou.

Brown and Amadon (1968) list small monkeys, opposums, and reptiles as the principal prey types. The data from this nest show a preponderance of reptiles, particularly while the male was principal provider for the family. One observation of the female atttacking a flock of Grey-winged Trumpeters (*Psophia crepitans*) passing near the nest suggest that birds are sometimes taken, although the foot structure and relative length of the toes are not typical of raptors that prey heavily on birds (Bierregaard 1978).

Concluding remarks.—As the observations reported here cover only a part of the breeding cycle, the dates for its initiation and completion can only be inferred. Assuming an incubation period of 40–50 days, laying probably took place between mid-February and mid-March, in the peak of the rainy season. Hatching occurred at the very beginning of the dry season. At the time of the last observation of the young, feathers were just appearing through the down on the back and upper wing coverts. The general appearance of the young on the last day it was observed (between 36 and 43 days after hatching) is very similar to that of the 54-day young Harpy Eagle pictured in the frontispiece of Rettig's (1978) study, in terms of the size relative to the parent and the feathers beginning to appear. The young harpy at the time was approximately 40% through the nestling phase. Had the young *Morphnus* survived and continued to develop at a similar rate, it would have fledged in the beginning of August, 90 days after hatching.

ACKNOWLEDGMENTS

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COLOR PLATE

The Frontispiece of the dark phase Guiana Crested Eagle (*Morphus guianensis*) has been made possible by an endowment established by George Miksch Sutton (1898–1982).

STUDENT MEMBERSHIP AWARDS IN THE WILSON ORNITHOLOGICAL SOCIETY FOR 1984

Student Membership Awards in The Wilson Ornithological Society have been made available from the general funds of the Society to recognize students who have the potential to make significant contributions to ornithology. The following students have been selected by the Student Membership Committee for awards this year: Robin Elizabeth Abbey, College of William and Mary; A. Margaret Elowson-Hawley, Univ. Wisconsin; Todd Eric Fink, Southern Illinois Univ.; Elizabeth Jane Hawfield, Winthrop College; Geoffrey Edward Hill, Univ. New Mexico; D. Scott Hopkins, Western Illinois Univ.; Shonah Anne Hunter, Southern Illinois Univ.; Jerry Wayne Hupp, Colorado State Univ.; Emily Dale Kennedy, Rutgers Univ.; Monica Grant LeClerc, Brigham Young Univ.; Nancy Ann Lutfy, Northern Illinois Univ.; Michael Richard North, North Dakota State Univ.; Andrew Townsend Peterson, Miami Univ. (Ohio); Eleanor Marie Prindiville, North Dakota State Univ.; Mark DuValle Reynolds, Univ. California (Berkeley); Kathryn Daniels Robinson, Bowling Green State Univ.; Elizabeth Irene Rogers, Michigan State Univ.; Greggory John Transue, Rutgers Univ.

Student Membership Committee—Thomas C. Grubb
Charles F. Leck
Roland R. Roth
John L. Zimmerman, *Chair*

Wilson Bull., 96(1), 1984, pp. 6–11

TUNDRA SWANS IN NORTHEASTERN KEEWATIN DISTRICT, N.W.T.

MARGARET A. MCLAREN AND PETER L. MCLAREN

Bellrose (1980) estimated that the total adult population of Tundra Swans (*Cygnus columbianus*) in the eastern Canadian Arctic (east of 90°W) in the 1960's was about 5000 birds. He also stated that continental populations (based on surveys of wintering areas) increased by 25% from then until 1976, with most of the increase occurring in Canadian nesting areas. More specifically, winter censuses by the U.S. Fish and Wildlife Service along the Atlantic coast revealed that numbers in 1976 were 22.4% higher than the average of the previous 10 years (R. M. Alison, pers. comm.). Assuming that numbers increased by the same proportion throughout the breeding range, about 6000 Tundra Swans nested in the eastern Canadian Arctic in 1976.

No one area of high swan abundance has been reported in the eastern Arctic to date. In this paper, we report the occurrence of a major concentration of nesting Tundra Swans in the lowlands adjacent to the Rasmussen Basin, Keewatin District, Northwest Territories, and comment on the reproductive success of this population.

THE STUDY AREA

The avifauna of the 'Rasmussen Lowlands' was studied during the summers of 1975 and 1976 as part of a series of similar studies along the route of a proposed natural gas pipeline. The Rasmussen Lowlands comprise an area of 9800 km² in northern Keewatin District (Fig. 1). It is an area of recent marine submergence, bounded to the west by Rasmussen Basin and Rae Strait, and to the north, east and south by landforms dominated by Precambrian rock. Vegetation consists primarily of graminoid communities dominated by *Carex* spp. and *Eriophorum* spp. Large numbers of small shallow lakes and ponds occur throughout. The area is crossed by the Inglis and the Murchison rivers, and numerous small tributaries.

In 1975, the land was snow-free and ice had left rivers, lakes, and ponds by 13 June, the date of our earliest survey. In 1976, the lowlands were 50–95% snow-covered when we arrived on 14 June. Lakes and ponds remained entirely frozen as did several of the channels in the Inglis-Murchison delta. A meltwater channel flowed over the ice of the Inglis River but the river itself remained frozen. The Murchison River was 50–80% open. Snow melt and ice melt occurred rapidly after 24 June and were virtually complete by 1 July.

Freeze-up occurred early in 1976. Many tundra ponds and parts of the major rivers were frozen by 27 August and very little open water remained by 17 September, our last survey. We have no information about freeze-up in 1975.

METHODS

Most of the work consisted of aerial surveys. In 1975, surveys were conducted by fixed-wing aircraft on 13–14 June and 28–29 August; surveys by helicopter were conducted on

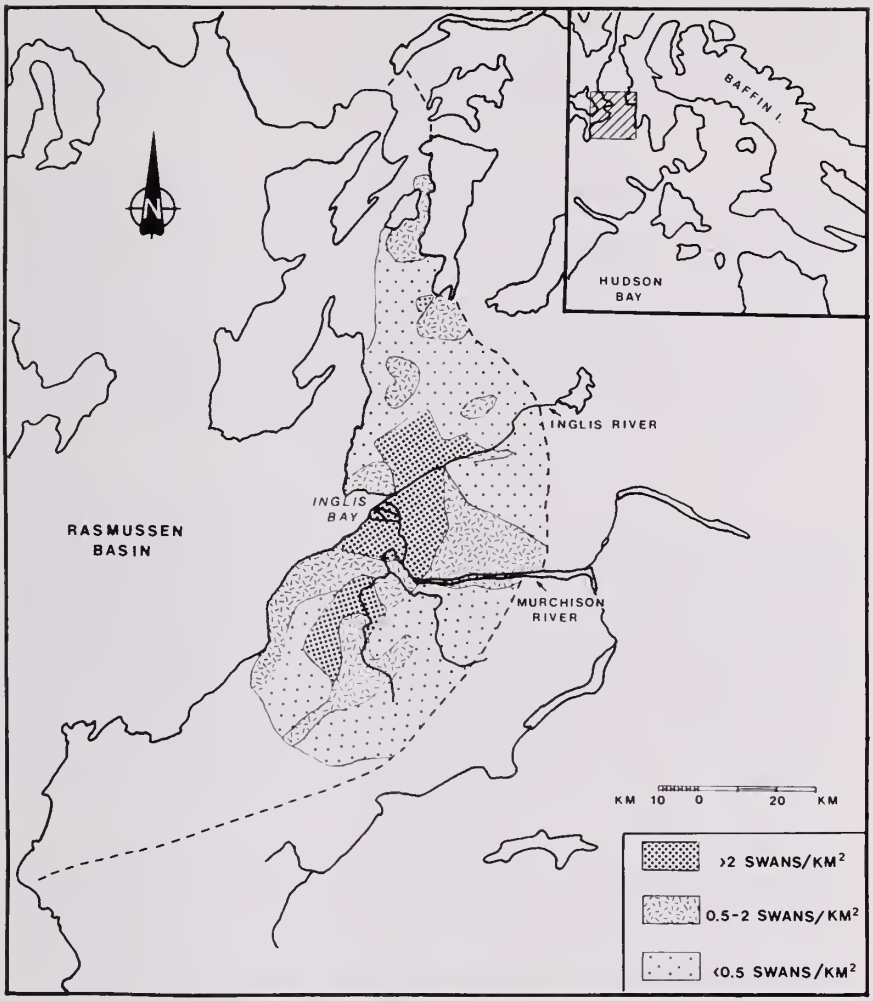

FIG. 1. Densities of nesting Tundra Swans in the Rasmussen Lowlands, N.W.T., Canada. The area between Rasmussen Basin and the dashed line includes about 9800 km²; the surveyed area includes 5846 km².

4–11 July. In 1976 fixed-wing surveys were conducted on 12–14 August, 27–28 August, and 17 September. Helicopter surveys were conducted in the period 20 June–15 July, including surveys of nesting swans conducted on 3–10 July. Fixed-wing surveys were flown at 30 m AGL and at 160 km/h.

Surveys for nesting swans were conducted from a Hughes 500-C helicopter. About 60% of the lowland area (5846 km²) was sampled (Fig. 1). Coverage was most intensive in habitats where we expected the highest densities of nesting birds. In general, our predictions were

TABLE 1

ESTIMATED NUMBERS OF ADULT TUNDRA SWANS IN THE RAMUSSEN LOWLANDS, KEEWATIN DISTRICT, N.W.T.

	Stratum					
	1	2	3	4	5	Total
Area (km^2)	565.5	1101.4	1428.9	1287.2	1463.2	5846.2
No. transects	17	30	31	18	24	120
No. km^2 surveyed	29.4	50.1	61.0	32.7	43.6	216.8
No. swans seen	17	93	20	50	5	185
Density (swans/km^2)	0.58	1.86	0.33	1.53	0.11	0.85
Estimated population[a]	385.1	2045.3	398.7	1968.8	167.8	4965.7
SE	143.7	431.2	104.8	484.5	82.0	677.5

[a] Apparent discrepancies between this line and density × area calculations are due to rounding error.

correct and the area was divided, a posteriori, based on habitat and distance from the coast, into five strata for analysis. Coverage in each stratum varied from 3–5%. Observers sat in the right front and left rear seats and dictated into tape recorders information about all birds seen. The helicopter flew at 50 km/h and 9 m above the ground. All birds seen within 100 m of the helicopter's path were considered to be on the transect strip. A total of 120 transects of average length 9 km was surveyed. Estimates of the adult swan population in the lowlands were based on sightings of single birds and pairs with no correction for the absent member in observations of singles. The population estimate for each stratum was calculated by the ratio estimate of Caughley (1977) for sampling without replacement for each stratum. The stratum estimates were then pooled to provide an overall estimate of the number of swans present and its standard error, following Cochran (1963) and Caughley and Grigg (1981).

RESULTS

The adult population of Tundra Swans in the 5846 km^2 sampled by our surveys was estimated to be 4966 ± 678 SE (Table 1). The overall density recorded was 0.85 swans/km^2 but the density was considerably higher in certain portions of the lowlands, especially in areas near the coast (Fig. 1). The highest average densities (>2 swans/km^2) occurred in the area inland from Inglis Bay.

In addition to adults, the lowlands support a substantial but unknown number of presumably immature swans in summer. We observed flocks of 14–70 of these swans primarily in the area east of Inglis Bay.

The late spring in 1976 affected brood size and the number of swans that nested, but did not appear to affect the timing of nest initiation substantially for those birds that did nest. We saw nesting swans during the first (13–14 June) survey in 1975 but no broods had been seen by the end of the 4–11 July survey period; 24 nests with eggs were found on 4–11 July. In 1976, despite considerably more extensive surveys, only 21 nests were found. The earliest cygnet in 1976 was seen on 2 July but no

others were seen until 12 July. We saw 50 broods in 2143.2 km of survey in late summer in 1975 and only 11 in 2724.3 km in 1976. Average brood size was significantly smaller in 1976 (2.48 in 1975 vs 1.63 in 1976; $P < 0.01$, Mann-Whitney U-test, N = 50, 11, $z = 2.39$).

DISCUSSION

We estimated that about 500 Tundra Swans nested to the southwest of the area that we surveyed systematically. Including those swans, we estimated that about 5500 adult Tundra Swans occur in the Rasmussen Lowlands. When combined with numbers of adult swans elsewhere in the eastern Arctic (about 800 birds) this value agrees remarkably well with the estimated number of 6000 adults in the eastern Arctic. Thus, the Rasmussen Lowlands appear to be the center of the eastern Arctic population. The center of the Tundra Swan population in the Rasmussen Lowlands is within about 25 km of the coast and from 25 km north to 25 km south of the Inglis River (Fig. 1).

Macpherson and Manning (1959) and Ryder (1971) both reported that Tundra Swans were already present at study areas 180 and 300 km, respectively, west of the Rasmussen Lowlands when research parties arrived in late May and early June. Observations of nesting swans in mid-June in this study also indicate a similar arrival date. Our earliest observation of a cygnet in the Rasmussen Lowlands was 2 July. Back-dating about 31 days to egg-laying (Bellrose 1980) and another week to arrival (Parmelee et al. 1967) indicates that the first adult swans had arrived about 23 or 24 May. The major influx is probably only slightly later.

The number of young produced by Tundra Swans in the Rasmussen Lowlands probably fluctuates widely among years. In terms of both number of broods and number of young per brood, 1975 was clearly much more successful than 1976. Fluctuation in nesting success between years is also typical of other areas. Lensink (1973) found that between 15% and 47% of the adult swans on territories in western Alaska produced young in any one year. Lensink (1973) also noted that the proportion of cygnets from the Yukon-Kuskokwim Delta surviving autumn migration was much greater in years with early springs than in years with late springs. He suggested that in more northerly areas, where shorter seasons are the rule, conditions for survival may be marginal.

In the Yukon-Kuskokwim Delta hatch did not begin later than 6 July but did begin as early as 20 June over 9 years of study (Lensink 1973). Although a cygnet was seen in the Rasmussen Lowlands as early as 2 July, the peak of hatch there does not occur until after 10 July. Cygnets are flightless for 60–75 days and thus the majority of young would not be able to begin migration until the latter half of September. In 1976, most swans departed from the Rasmussen Lowlands during the first 2

weeks of September but families were still present on 17 September when only the ocean and small patches of the Murchison River remained ice free. The young of these families were still flightless (pers. obs.). Comparison of mean daily temperatures for the Yukon-Kuskokwim Delta and the Rasmussen Lowlands suggests a precarious existence for swans in the latter area. Mean daily temperatures in May and September in the Rasmussen Lowlands are −10.1°C and −1.1°C, respectively (Anon. 1982). In the Yukon-Kuskokwim Delta, temperatures in May and September average about 2°C and 6–8°C, respectively (Brower et al. 1977).

Conditions for survival of the Tundra Swan population in the Rasmussen Lowlands are probably not optimal. Late springs result in nonbreeding by a substantial proportion of the population and small broods for pairs that do breed. Most cygnets hatch after 10 July in both good and bad years and the length of the fledgling period is such that they cannot leave the lowlands before consistent freezing temperatures occur.

SUMMARY

Tundra Swans (*Cygnus columbianus*) in the lowlands adjacent to the Rasmussen Basin, Keewatin District, N.W.T., were counted during fixed-wing and helicopter surveys in 1975 and 1976. The lowlands support an estimated population of 4966 ± 678 SE nesting swans and we estimated an additional 500 nesting swans to the southwest in an adjacent area that we did not survey systematically. Since only 6000 Tundra Swans are estimated to nest in the eastern Canadian Arctic, the Rasmussen Lowlands appear to be the center of abundance in this region for the species. Flocks of presumably immature swans also occur in the lowlands in summer.

Spring was much later in 1976 than in 1975. Fewer Tundra Swans nested in 1976 and the broods of those that did nest were significantly smaller than broods in 1975 ($P < 0.01$). In both years the peak of hatch occurred after 10 July and, at least in 1976, family groups with flightless young were observed when freeze-up of freshwater was almost complete. The short summer season in the Rasmussen Lowlands in comparison with other areas with high densities of nesting Tundra Swans suggests that conditions for survival of this lowland population are less than optimal.

ACKNOWLEDGMENTS

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LGL LTD., ENVIRONMENTAL RESEARCH ASSOCIATES, 414–44 EGLINTON AVE. W., TORONTO, ONTARIO M4R 1A1, CANADA. ACCEPTED 10 SEPT. 1983.

HAWK MOUNTAIN RESEARCH AWARD

The Hawk Mountain Sanctuary Association is accepting applications for its 8th annual award for raptor research. To apply for the $500 award, students should submit a description of their research program, a curriculum vita, and two letters of recommendation by 30 September 1984, to James J. Brett, Curator, Hawk Mountain Sanctuary, Rt. 2, Kempton, Pennsylvania 19529. The Association's Board of Directors will make a final decision late in 1984. Only students enrolled in a degree-granting institution are eligible. Both undergraduate and graduate students are invited to apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.

Wilson Bull., 96(1), 1984, pp. 12–19

RING-BILLED GULLS DISPLAY SEXUALLY TOWARD OFFSPRING AND MATES DURING POST-HATCHING

PETER M. FETTEROLF

While studying Ring-billed Gulls (*Larus delawarensis*) during post-hatching on Mugg's Island, Toronto, Ontario, Canada, I observed adult gulls with offspring performing pre-copulatory and copulatory behavior toward both their young and their mates. Kinkel and Southern (1978) documented three cases of adult female Ring-billed Gulls sexually "molesting" pre-fledging young. Here, I present data on adult-adult and adult-chick sexual interactions, examine associated ecological and behavioral parameters, and discuss the possible proximate causes and functions of these interactions.

METHODS

Description of the site, location of the observation blind and the study plots, and methods for collection of data are briefly reviewed here and given in detail elsewhere (Fetterolf 1979, 1981, 1983). A blind adjacent to three study plots (7 × 14 m) was located near the geographic center of the oval-shaped colony of about 6000 nesting pairs. During the incubation period in all years (1976–1978), nests were labeled with numbered tongue depressors placed near nest rims and nest locations were mapped. The onset of hatching in each nest was determined during visits (to all plots in 1976 and one plot in 1977) or from the blind (for one plot in 1977 and all plots in 1978). From the blind in each year I determined the number of young that fledged (reached 35 days of age).

Ecological parameters.—After the gulls left the site in August, my assistant and I measured five nest-site characteristics (see Fetterolf 1981, 1983). The birds nested in clumps (see Vermeer 1970) and each plot had one or two clumps of nesting birds. I therefore designated birds with no nearby neighbors in one of the major compass quadrants as edge nesters and others as center nesters. Nearby nests are defined as those located within 3 m of a study nest, without intervening nests—that is, there can be only one nearest neighbor along any single line radiating from a single nest. I recorded territory size for nesting pairs in 1976 and 1978 by mapping the location of agonistic encounters between neighbors for each of two subsequent observation days. I quantified the hatching synchrony of each pair with its nearby neighbors by averaging the absolute values of the differences between the hatching date of the first egg of the subject pair and each of its neighbors.

Behavioral parameters.—From the blind, I collected data on adult-adult agonistic behavior, adult attacks on neighboring chicks, intraspecific kleptoparasitism, food provisioning of young, food-begging by chicks, food-begging by adults, and sexual behavior by adults between 15:30 and dark (about 21:00) every second evening. At about 04:30 the morning after spending the night in the blind, I sampled behavior for approximately 5 h. I recorded adult-adult agonistic behavior during 1-min random samples (Fetterolf 1981). All other behaviors mentioned above were noted whenever I saw them and were standardized by dividing by the number of hours of observation for each pair.

Adults and chicks stole food from neighbors infrequently during 1976 and frequently during the last 2 years of the study (see also Elston et al. 1978). I recorded the identity of

the thief and victim whenever possible. I quantified the frequency of robbing by the pair and from the pair. In 1977 and 1978, I counted each feeding by parents and noted the type and amount of food. In 1978, I also estimated the size of food items (about 75% fish) and computed the amount of biomass fed to each brood using regression equations of body weight vs body length for each fish species (J. R. Foster, pers. comm.).

Chicks beg for food by "head-tossing" and by uttering a high-pitched vocalization similar to the adult "head-tossing call" (see below) (Moynihan [1955] for the Black-headed Gull [*L. ridibundus*] and Hailman [1967] for the Laughing Gull [*L. atricilla*]). Whenever chicks in a brood begged for more than 4 min, I counted it as a protracted begging bout. Sometimes adults head-tossed, uttered the associated call, and "robbed" food from their brood while the mate provisioned young. I counted each incident as mate food-begging.

During courtship, sexual displays usually occur in the following order: head-tossing, "copulation call," mounting, and copulation (Moynihan 1958, Southern 1974, Fetterolf 1979). Head-tossing can be performed by both sexes and is characterized by a series of rapid skyward bobs of the bill accompanied by the head-tossing call. The copulation call is typically a male courtship behavior which precedes mounting and can be described as a rapid *ka ka ka* (Southern 1974). Mounting occurs when one individual hops onto the other's back, and copulation ensues when the mounted bird lowers its tail to make cloacal contact. Occasionally, a thwarted mounting or copulation is followed by "tail waggling" (Moynihan [1955] for Black-headed Gull).

Determination of gender.—For each nesting pair, I assigned a gender to each gull using sexual behavior observed during pre-egg-laying, body size (Ryder 1978), head shape (male has less rounded head), and bill length and depth (Ryder 1978). I tested my ability to subjectively determine the sex of Ring-billed Gulls in 1980 and 1981 at the Eastern Headland in Toronto. Colleagues and I trapped 201 gulls in a drop trap (Mills and Ryder 1979) and sexed them using bill measurements (Ryder 1978). Prior to handling the birds, I guessed the gender of each bird from a distance using binoculars. I correctly sexed 97.5% of the birds.

Data analysis.—In 1976, because I concentrated on other research, my records of sexual behavior are probably incomplete. For the first half of 1976, I incorrectly assumed that males were displaying sexually toward chicks. I therefore excluded all 1976 data from the analyses of ecological and behavioral parameters associated with sexual behavior and only report the actor's gender in 1977 and 1978.

I divided the data for adult-adult and adult-chick sexual behavior into two groups: (1) pairs in which at least one individual exhibited sexual behavior (hereafter sexual pairs); and (2) pairs in which no sexual behavior was observed (hereafter non-sexual pairs). Sample sizes were small for sexual pairs in each year (Tables 1, 2) and there were no significant differences ($P < 0.05$) in variance between years (F test). I therefore combined the data and analyzed them with two-tailed t-tests. Whenever an F test indicated a significant difference in variance between sexual and non-sexual pairs for any ecological or behavioral parameter, I used a t-test and calculated a reduced number of degrees of freedom (Dixon and Massey 1969).

RESULTS

Adult-adult sexual behavior.—Fifteen of the 421 (3.6%) pairs that reared young throughout the study (Table 1) engaged in sexual behavior during the post-hatch period. One pair engaged in sexual behavior on three occasions, one pair on two occasions, and 11 pairs exhibited such behavior only once. In all instances of adult-adult sexual behavior, females initiated

TABLE 1
ADULT-ADULT SEXUAL BEHAVIOR FOR RING-BILLED GULLS DURING POST-HATCHING 1976–1978

Year	No. pairs observed	No. incidents		No. pairs involved
		Morning	Evening	
1976	139	3	1	4
1977	156	6	4	7
1978	126	3	2	4
Total	421	12	7	15

head-tossing while the mate provisioned chicks. The age of the oldest chick in each brood ranged from 3–30 days ($\bar{x}$ = 18.84, SD = 8.86, N = 19) when each incident occurred. Males copulation-called while females head-tossed. Males mounted females and performed copulatory tail-lowering during 15 (78.9%) of 19 incidents. Females often ran out from under the male or tried to force him to dismount by pecking violently at his breast. Following copulation, females continued head-tossing and on two occasions were fed by the male. Females were never observed performing copulation call or mounting toward mates but on three occasions they "food-begged" by pecking at the base of the male's bill (Moynihan 1958).

No ecological parameters were significantly different for pairs that engaged in adult-adult sexual behavior and those that did not. Pairs that engaged in sexual behavior performed mate food-begging ($\bar{x}$ = 0.035 per h, SD = 0.031) significantly more often than pairs not involved in sexual activity ($\bar{x}$ = 0.006, SD = 0.011, t = 7.79, df = 10, $P < 0.001$). Ninety one of 156 (58.3%) incidents of mate food-begging in 1977 and 1978 involved females (χ^2 = 4.33, df = 1, $P < 0.05$).

Adult sexual behavior toward chicks.—From 1976–1978, 38 of 842 (4.5%) adults performed copulation call, mounting, tail waggling or copulation toward chicks (Table 2). Based on the number of hours of observation (53% in the morning), more incidents were observed in the evening than the morning (χ^2 = 4.75, df = 1, $P < 0.05$). In 1977 and 1978, 55 of 58 (94.8%) instances of sexual behavior involved adult females as actors (χ^2 = 39.10, df = 1, $P < 0.001$) even though males were on the territory during 46% of all 1-min random samples.

Adults directed sexual displays at their own offspring on 64 (91.4%) of the 3-year total of 70 incidents. Thirty six (51.4%) of these incidents led to copulation with the chick; the remainder included copulation call and often attempted mounting or tail waggling (Table 2). Ten individuals

TABLE 2

ADULT SEXUAL BEHAVIOR OF RING-BILLED GULLS TOWARD CHICKS 1976–1978

Year	No. incidents		Actor's sex		No. adults involved	Behavior			
	Morning	Evening	Male	Female		Copulation call only	Copulation call, mounting attempt	Copulation call, tail waggling	Copulation
1976	4	8	—	—	6	1	1	1	9
1977	16	24	2	38	17	7	6	13	14
1978	8	10	1	17	15	4	1	0	13
Total	28	42	3	55	38	12	8	14	36

displayed toward chicks on two or more occasions and one female behaved sexually toward its offspring 11 times. Sexual displays were performed toward chicks ranging in age from 9–44 days ($\bar{x} = 21.1$, SD = 7.63, N = 70). Chicks were begging from the adult before and during all but eight cases of sexual behavior. When begging, chicks circled around and close to the displaying adult, much as a female head-tosses to her mate during the pre-egg-laying period. Chicks sometimes avoided mounting by circling more rapidly. When mounted, chicks sat down giving a distress vocalization until the adult dismounted. Occasionally the chick then began to beg again. On eight occasions chicks were sitting and silent when adults displayed sexually toward them. In six of these eight cases, the adults involved displayed sexually toward unguarded neighboring chicks rather than their own offspring.

Only one ecological parameter, the number of nearby neighbors, was significantly related to sexual behavior toward chicks. Pairs that displayed sexually toward chicks had more nearby neighbors than pairs that did not ($t = 3.13$, df = 280, $P < 0.001$) (Table 3). The former also had significantly more observed chick feedings ($t = 3.49$, df = 35, $P < 0.001$), more frequent protracted chick begging ($t = 3.26$, df = 33, $P < 0.01$) and more frequent mate food-begging ($t = 2.70$, df = 280, $P < 0.01$) than the latter. Unlike mate food-begging and adult-adult sexual behavior, sexual displays toward chicks were not associated with provisioning of young. Food-robbing from neighbors was also more common for sexual pairs than for non-sexual pairs ($t = 3.25$, df = 32, $P < 0.01$).

DISCUSSION

Apparently, begging for food by a mate or chick sometimes elicited a sexual rather than a feeding response from the accompanying adult. Play-

TABLE 3

VARIABLES WHICH DIFFERED ($P < 0.01$) BETWEEN SEXUAL (N = 31 PAIRS) AND NON-SEXUAL PAIRS (N = 251) FOR COMBINED 1977 AND 1978 DATA

Type of pair	No. nearby neighbors	No. feedings observed/h	Protracted chick begging/h	Mate begs food	Attempted thefts by pair/h
Sexual behavior toward chicks	4.74 ±1.26[a]	0.072 ±0.055	0.0038 ±0.0067	0.013 ±0.015	0.019 ±0.039
No sexual behavior toward chicks	4.06 ±1.14	0.044 ±0.040	0.0012 ±0.0039	0.006 ±0.013	0.007 ±0.015

[a] SD.

backs of the adult head-tossing call during pre-egg-laying demonstrate that this vocalization stimulates sexual behavior in males and females (Fetterolf and Dunham, unpubl.). Pairs that engaged in adult-chick sexual behavior had more nearby neighbors. Perhaps more neighboring chicks provided more auditory stimulation which promoted sexual behavior.

The associations among sexual behavior, begging by mates for food during provisioning of young, and begging by chicks when feeding was not imminent, supports the interpretation that food stress promoted sexual behavior. Male gulls that engaged in sexual display toward mates were paired with females that begged more often when food was offered to chicks and these pairs attempted to rob food from neighbors more than gulls that did not display sexually. Female gulls that displayed sexually toward chicks begged food more often during provisioning of young and reared chicks that begged for more protracted periods when feeding was not imminent. Begging by mates often preceded robbing of food from the brood; robbing is probably a sign of food stress (Elston et al. 1978, Brockmann and Barnard 1979). Glaucous-winged Gull (*L. glaucescens*) chicks increased their begging when deprived of food for long periods suggesting that chick begging is an indicator of food stress (Henderson 1975). Sexual behavior toward chicks occurred more frequently during my evening sampling periods when young were more likely to be food-stressed. Chick provisioning is most frequent in early morning and late evening (Kirkham and Morris 1979) and chicks are not fed very often for periods of 8–10 h during the day. Most of my evening sampling sessions preceded late evening provisioning whereas most morning samples followed feeding.

More frequent chick feedings by pairs which displayed sexually toward chicks seems to contradict the food stress interpretation. However, males

often do most of the foraging, sometimes leaving females on the territory for periods extending over two or more male foraging trips (Fetterolf, unpubl.). These long periods of female presence on the territory often preceded mate food-begging which was more frequent for females than males. Females also performed nearly all sexual behavior toward chicks. Thus, the data are compatible with the hypothesis that food-stressed female gulls elicited sexual behavior from mates and performed sexual behavior toward chicks.

As Kinkel and Southern (1978) commented, it is especially interesting that females performed sexual behaviors indistinguishable from those of courting males. Hunt and Hunt (1977) reported that three female Western Gulls (*L. occidentalis*), in pairs consisting of two females, performed male behaviors such as copulation (see also Wingfield et al. 1982). Female-female pairs occur in Ring-billed Gulls (Ryder and Somppi 1979, Conover et al. 1979), although it has not been reported whether females perform male sexual behavior in these pairs.

It is possible that sexual behavior toward chicks is nonadaptive or maladaptive even though chicks did not appear to be harmed by mounting. However, such behavior in fact may be adaptive because it allows parents to control the behavior of their offspring while minimizing the chances of harming them. Persistent begging by chicks was characteristic of all behavioral sequences leading up to sexual displays by adults and seemed to 'agitate' the parent. The parent had three possible responses: (1) it could endure the harassment; (2) it could leave the territory; or (3) it could try to stop the chick's begging. Prolonged chases around the territory could be energetically costly for both parent and young. Parental absence from the territory exposes the offspring to attacks by neighbors (Fetterolf 1983). If a parent pecks at its own chick to silence it, the parent risks chasing its offspring from the territory and thus subjecting it to attacks by other gulls (Fetterolf 1983). Display of the orange mouth lining during copulation call probably functions as a threat during adult courtship (Fetterolf 1979). This display, sometimes in combination with mounting, may thus provide a low-risk means for female parents to control the behavior of their offspring.

SUMMARY

From 1976–1978, I quantified the sexual behavior of adult male and female Ring-billed Gulls (*Larus delawarensis*) rearing chicks. Male Ring-billed Gulls occasionally displayed sexually to their mates and rarely exhibited such behavior toward their chicks. However, females frequently performed sexual behavior toward their offspring which was indistinguishable from the sexual behavior of courting males. Males exhibited sexual behavior toward their mates when females begged for food during feedings of offspring. Persistent

begging by chicks when feeding was not imminent apparently stimulated females to perform male-like behavior toward them. Females that engaged in sexual behavior with mates or chicks may have been food-stressed.

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RAPTOR COLLISIONS WITH UTILITY LINES

A Call for Information.—The U.S. Bureau of Land Management, Sacramento, in cooperation with the Pacific Gas and Electric Company, is assembling all available published and unpublished information concerning collisions of raptors with power lines and other utility lines. Actual case histories—no matter how circumstantial or fragmentary—are needed. Please acknowledge that you have such information by writing to Dr. Richard R. (Butch) Olendorff, U.S. Bureau of Land Management, 2800 Cottage Way, Sacramento, California 95825 U.S.A. (Phone (916) 484-4541). A form on which to record your information will then be sent by return mail.

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WINTER TERRITORIALITY IN LESSER SHEATHBILLS ON BREEDING GROUNDS AT MARION ISLAND

ALAN E. BURGER

There is an expanding literature on the adaptiveness of social behavior outside the breeding season, particularly in shorebirds. Most studies have dealt with birds foraging solitarily or in flocks (e.g., Evans 1976, Silliman et al. 1977, Sutherland and Koene 1982) or in territories on wintering grounds (e.g., Myers et al. 1979a,b; 1981). There is less known about birds defending breeding territories outside the breeding season. Territoriality is generally viewed as an adaptation facilitating the use of certain limiting resources to improve the individual's fitness (Brown 1964, Brown and Orians 1970, Davies 1978). Since territorial behavior usually incurs some cost, there should be evidence that territoriality outside the breeding season enhances the survival of an individual or its close relatives and/or enhances subsequent breeding opportunities. In this study, I have examined ways in which territoriality during the winter non-breeding season might benefit Lesser Sheathbills (*Chionis minor*) on sub-Antarctic Marion Island (46°54′S, 37°45′E) in the Indian Ocean.

Sheathbills are opportunistic predators and scavengers found in parts of the Antarctic and sub-Antarctic (Watson 1975). At Marion Island, the birds ate a wide range of food in several habitats, but were primarily dependent on food from penguin colonies during the breeding season (Burger 1981a, b). Breeding adults maintained territories centered on penguin colonies during the summer breeding season (November–mid-March), in which they foraged and nested (Burger 1979, 1980a; Burger and Millar 1980). Territories within colonies of Rockhopper (*Eudyptes chrysocome*) and Macaroni (*E. chrysolophus*) penguins were abandoned during the austral winter (April through October), when these penguins deserted the island. The sheathbills then foraged solitarily or in flocks on the shoreline or the vegetated coastal plain and some moved to colonies of King Penguins (*Aptenodytes patagonicus*) (Burger 1981a, 1982). King Penguins were present at the island throughout the year and the carcasses of chicks and adults provided food for sheathbills all winter (Williams et al. 1978). Sheathbills also kleptoparasitized those King Penguins which continued to feed chicks during the winter.

About 48% of the 3500 sheathbills at Marion Island foraged in King Penguin colonies in winter (Burger 1981a). Sheathbill pairs which bred in these colonies in summer remained territorial all year. Territorial defense, involving both sexes, appeared to be equally vigorous in winter

and summer (Burger 1980a, Burger and Millar 1980). Breeding adults retained the same mates and territories from season to season and had an annual survival of 88% (Burger 1979) and so the adults defending winter territories probably bred there the following summer. I compared the time budgets and diets of territorial and non-territorial sheathbills wintering in a King Penguin colony to determine the effects of territoriality.

METHODS

Observations were made at a colony of King Penguins at Archway Bay, Marion Island in early winter (21 April–10 May 1978). These observations were supplemented with others from a larger study at the same site, from 1974–1978 (Burger 1979; 1980a,b; 1981a; Burger and Millar 1980). The colony contained 1000 adult penguins and 1200 chicks as well as 40–50 sheathbills. The sheathbills' territorial boundaries were known and most of the resident birds were color-banded.

Three categories of sheathbills were recognized: territorial adults, intruders, and juveniles. There were 12 pairs of territorial adults; all of those observed were color-banded, paired, and known to have bred in their territories. There were variable numbers (10–20) of intruders, mostly subadults (Burger 1980b) in their second or third winters, but also including non-territorial adults. These birds visited the colony to forage in undefended fringe areas and by intruding into the territories. Juveniles were 3–4 months old and independent of their parents. They were tolerated within their parents' territories where they did most of their foraging. All the juveniles and all but two intruders observed were either color-banded or marked with small dabs of picric acid solution. Since parents and juveniles were all marked, family relationships were accurately determined.

Focal animal observations (Altmann 1974) were made of sheathbills actively foraging in the penguin colony and the adjacent beach. Sheathbills were unafraid of people and were studied with the aid of binoculars and a tape recorder while I sat quietly at 20–60 m range. Temperatures varied from −2–5°C and there were occasional ice squalls. Each focal observation lasted 30 min. Three males, three females, two intruders, and two juveniles were each watched for two periods, all other birds once. The duration and frequency of behaviors were measured from recorded commentary using stopwatches and tally-counters. Handling and eating time (Schoener 1971), hereafter referred to as "eating," included time to swallow, pull bits off carcasses, extract invertebrates from the substrate, and wait next to penguins for opportunities to kleptoparasitize them. "Walking" included searching and movements between food sources. The rate of swallowing was used as a rough means of comparing the intake of similar foods between birds.

Instantaneous-scan observations (Altmann 1974) were used to provide estimates of time spent foraging (eating, walking and other activities while seeking food), resting, preening, and displaying from dawn to dusk (06:00–17:20) on 21 April 1978. Observations were made from a raised vantage point and scans made every 5 min. It was not possible to record the sex, age or status of birds at each scan.

Body weights and annual survival rates were analyzed to determine whether juveniles living in the King Penguin colony fared better than those living elsewhere. Body weights of live birds were measured between 1974–1978, as described by Burger (1980b). Annual survival was estimated from recaptures and sightings of banded birds, between 1974–1976 (see Burger 1979 for methods).

Standard deviations are given with means. Non-parametric Mann-Whitney *U*-tests were

used to analyze the focal-animal data. Student's *t*-tests were used to analyze the duration of feeding bouts at carcasses, where the sample sizes were large.

RESULTS

Agonistic encounters between sheathbills at the King Penguin colony consisted mostly of chases (Burger 1980a, Burger and Millar 1980). These ranged from low intensity encounters where one bird supplanted another at a food source, to vigorous chases of 10–20 m involving rapid running and often flapping flight as a territorial adult evicted an intruder from its territory. Although chasing and being chased used little of the foraging time (Table 1), these activities disrupted the birds' foraging; at a rate of once every 5 min for territorial adults and juveniles, and every 2 min for intruders (Table 2). Territorial males and females were rarely chased by other birds, and they spent significantly more time chasing and less being chased, than either intruders or juveniles (Tables 1 and 2). Although the juveniles were subordinate to the intruders, which were older birds, the juveniles were chased for significantly less time (Table 1) and far less frequently (Table 2) than intruders, with fewer disruptions to their foraging. Juveniles reduced agonistic encounters by foraging within their parents' territories. Those that strayed outside their parents' territories were regularly chased by neighboring territorial adults, intruders and other juveniles. Adults quite frequently chased their own offspring, but these chases were brief, usually supplantings, and the offspring were not driven out of territories at this time.

Sheathbills ate four recognizable food types in the King Penguin colony. Food kleptoparasitized from the penguins (hereafter referred to as "penguin food") and flesh from carcasses were food of high quality. Penguin food consisted of fish, squid, and marine crustaceans stolen from penguins as they regurgitated to their chicks (Burger 1979). Penguin food had an energy content of 4.5–6.8 kJ g^{-1} (fresh weight) and a protein content of 14–18% of fresh weight (Burger 1981a). When a sheathbill was successful at robbing a penguin, the mass of food ingested per peck appeared to be about 10× that of other food.

The colony was littered with numerous carcasses of penguins, virtually all within sheathbills' territories. All that remained of most carcasses was skin and bones. Sheathbills generally gained access to a carcass only after the skin had been ripped off and most of the flesh eaten by Southern Giant-Petrels (*Macronectes giganteus*), Northern Giant-Petrels (*M. halli*) and Brown Skuas (*Catharacta lonnbergi*). Sheathbills picked off small pieces of meat, skin and blubber, which had energy contents of 4.9–11.6 kJ g^{-1} and protein contents of 13–19% of fresh weight (Burger 1981a).

Invertebrates taken from the Penguin colony represented food of in-

TABLE 1

MEAN (± SD) PERCENTAGE OF TIME SPENT BY LESSER SHEATHBILLS IN VARIOUS ACTIVITIES WHILE FORAGING IN A KING PENGUIN COLONY

Activity	Territorial males (M) (N = 10)	Territorial females (F) (N = 10)	Intruders (I) (N = 14)	Juveniles (J) (N = 10)	Significant differences[a]
Eating	45 ± 13	52 ± 18	29 ± 15	49 ± 17	M > I (U = 108), F > I (U = 122), J > I (U = 112)
Walking	44 ± 12	34 ± 18	57 ± 13	40 ± 17	I > M (U = 109), I > F (U = 119), I > J (U = 111)
Looking around	8 ± 12	11 ± 7	11 ± 6	8 ± 5	No differences
Chasing	2.1 ± 1.5	1.4 ± 1.2	0.4 ± 0.6	0.4 ± 0.7	M > I (U = 133), F > I (U = 104), M > J (U = 80), F > J (U = 76)
Fleeing	0.0	0.1	3.3 ± 2.0	0.8 ± 0.7	I > M (U = 140), J > M (U = 80), I > F (U = 14), J > F (U = 95), I > J (U = 133)
Threatening	0.6 ± 1.9	0.2 ± 0.2	0.3 ± 0.6	0.0	Not tested
Pair display	0.3 ± 0.3	1.4 ± 1.2	0.0	0.0	Not tested
Preening	0.7 ± 1.1	0.8 ± 0.8	0.9 ± 1.1	0.3 ± 0.4	No differences
Soliciting food	0.0	0.0	0.0	3.2 ± 2.5	Not tested
Mean observation time (min)	30 ± 1	28 ± 3	25 ± 5	28 ± 4	

[a] Mann-Whitney U-test, $P < 0.05$.

TABLE 2

MEAN (± SD) RATE OF AGONISTIC EVENTS (PER H) BY SHEATHBILLS IN A KING PENGUIN COLONY

Behavior	Territorial males (M) (N = 10)	Territorial females (F) (N = 10)	Intruders (I) (N = 14)	Juveniles (J) (N = 10)	Significant differences[b]
Chasing	15.6 ± 8.4 (99)[a]	13.4 ± 11.5 (69)	3.9 ± 4.8 (25)	3.0 ± 5.4 (22)	M > I (U = 127), M > J (U = 92), F > I (U = 104), F > J (U = 78)
Being chased	0 (0)	0.2–0.8 (3)	28.2–10.3 (184)	10.2–9.6 (89)	I > M (U = 140), I > F (U = 140), J > M (U = 80), J > F (U = 80)
Both combined	15.6 ± 8.4 (99)	13.6 ± 11.7 (72)	32.0 ± 12.9 (209)	13.2 ± 9.8 (111)	I > M (U = 120.5), I > F (U = 120), I > J (U = 127)

[a] Figures in parentbeses show the numbers of encounters observed.
[b] Mann-Whitney U-test, $P < 0.05$.

termediate quality, averaging 3.0 kJ g^{-1} and 11% protein (Burger 1981a). Small flies (Diptera), Collembola and mites (Acarina) were widely distributed across the colony. Larger kelp flies (*Paractora* sp. and *Apetenus* sp.), their larvae and pupae and small oligochaetes occurred within rotting kelp on the beach and colony floor and were quite abundant in patches. Use of invertebrates by sheathbills involved considerable search time spent walking, but negligible handling time.

Freshly voided excreta from penguins represented low quality food, averaging 2.1 kJ g^{-1} and 3% protein (Burger 1981a). The sheathbills did not appear to seek this food actively but ate it opportunistically as they walked about the colony. In addition to the above food types, the sheathbills also ate unidentified small items, which were probably tiny arthropods, excreta and the fragments of blood-sheaths shed from the feathers of molting penguins.

The instantaneous-scan observations revealed that the sheathbills spent 69% of the day foraging, 21% resting, 9% preening, and displaying ($N = 45 \pm 4$ birds per scan). Ninety percent of the foraging birds were located among the penguins, 8% on piles of rotting kelp jetsam, and 2% on small patches of vegetation within and bordering the colony. The sheathbills' territories covered most of the penguin colony and the adjacent beach. Non-territorial birds moved away from these areas to rest and preen and almost all agonistic encounters involved foraging birds.

Focal-animal observations revealed that foraging birds performed several activities, but eating, walking and looking around made up 97% of the foraging time of each class of sheathbill (Table 1). Of these major activities, intruders spent significantly less time eating, but more walking, than the territorial adults and juveniles but there were no other significant differences (Table 1). Since the rates of food intake by intruders were not higher than the other birds (see below), but their eating time was less, these data suggest that the intruders had to spend more of the day foraging than other birds. Sheathbills frequently raised their heads to look about. This probably had at least two functions: to look for new feeding opportunities and to watch for skuas which foraged in the penguin colony and occasionally attacked sheathbills (Burger 1979). Agonistic behavior, pair displays and brief intervals of preening took little of the foraging time (Table 1). Juveniles spent 3% of their foraging time soliciting food from their parents, an activity which yielded negligible amounts of food. This behavior was also an appeasement signal (Burger 1980a).

The percentage of foraging time spent eating each food type (Table 3) and the rates of swallowing (Table 4) were used to indicate the sheathbills' access to the food types and a rough measure of food intake. With the exception of penguin food, all bird classes ate all food types and most individuals included all types of food in their diets.

TABLE 3

MEAN (± SD) PERCENTAGE OF FORAGING TIME SPENT EATING VARIOUS FOOD TYPES[a]

Food type	Territorial males (M)[b]	Territorial females (F)	Intruders (I)	Juveniles (J)	Significant differences[c]
Penguin food	12 ± 15 (30)	10 ± 17 (30)	4 ± 12 (7)	0	Not tested (see text)
Carcass	20 ± 22 (90)	39 ± 26 (100)	18 ± 18 (93)	31 ± 22 (100)	F > I ($U = 112$)
Invertebrates	10 ± 21 (80)	1 ± 1 (70)	2 ± 2 (86)	2 ± 5 (80)	No differences
Excreta	2 ± 2 (90)	1 ± 2 (70)	2 ± 1 (93)	4 ± 4 (80)	No differences
Unidentified objects	1 ± 1 (100)	1 ± 1 (100)	3 ± 2 (100)	12 ± 15 (100)	I > M ($U = 110$), I > F ($U = 126$), J > M ($U = 75$), J > F ($U = 85$)
Total eating	45 ± 13	52 ± 18	29 ± 15	49 ± 17	

[a] Sample sizes as in table 1.
[b] Figures in parentheses show the percentages of birds eating the foods.
[c] Mann-Whitney U-test, $P < 0.05$.

TABLE 4

MEAN (± SD) RATES OF SWALLOWING FOOD (SWALLOWS/MIN OF FORAGING TIME) BY SHEATHBILLS

Food type	Territorial males (M) (N = 10)	Territorial females (F) (N = 10)	Intruders (I) (N = 14)	Juveniles (J) (N = 10)	Significant differences[a]
Penguin food	0.2 ± 0.5	0.2 ± 0.5	0.1 ± 0.3	0	Not tested (see text)
Carcass	11.2 ± 14.5	25.4 ± 26.3	7.4 ± 7.3	16.2 ± 15.0	F > I (U = 110)
Invertebrates	1.1 ± 2.2	0.3 ± 0.6	0.6 ± 0.7	0.6 ± 1.2	I > F (U = 109)
Excreta	0.7 ± 0.6	0.4 ± 0.6	0.8 ± 0.6	1.3 ± 1.1	J > F (U = 77)
Unidentified objects	0.8 ± 0.3	0.6 ± 0.4	1.9 ± 1.0	3.7 ± 3.6	I > M (U = 120), I > F (U = 125), J > M (U = 79), J > F (U= 82)

[a] Mann-Whitney U test, $P < 0.05$.

Territorial males and females appeared to spend more time attempting to rob penguins, and were seemingly more successful at this activity than were the intruders. Sample sizes were too small for statistical testing (Tables 3 and 4). During 20 observation periods involving territorial adults, four males and four females (40% of the adults) actually leapt against the penguins to disrupt their feeding of chicks, and three males and three females (30%) obtained food in this manner. By contrast, only two intruders (14% of 14 records), both non-territorial adults, leapt against the penguins but only one (7%) was successful in obtaining food. The only sheathbills which obtained appreciable amounts of food by kleptoparasitism (10 swallows or more per 30 min focal-watch) were those which devoted 30% or more of their foraging time to this task. Successful sheathbills regularly had to spend long periods (>1 min) watching for the right moment to disrupt a penguin as it delivered food to its chick. Territorial adults, which could stand for long periods without being chased by conspecifics, had an advantage in getting penguin food over intruders, which were frequently chased. No juveniles attempted to rob penguins.

The sheathbills spent most of their eating time and obtained most of their food at carcasses. Territorial females spent significantly more time and had higher rates of swallowing at carcasses than intruders, but there were no other significant differences between other sheathbill classes (Tables 3 and 4). The swallowing rate by males at carcasses was higher than intruders but not significantly so. This was partially due to the fact that in 5 of the 10 observations, the males appeared to concentrate on getting penguin food or large invertebrates, rather than food from carcasses.

Territorial adults were dominant at all carcasses within their territories and tended to feed on fresher carcasses, which yielded larger portions per peck, than those normally accessible to intruders. Territorial males were never chased during feeding bouts at carcasses (N = 65 bouts) and territorial females were chased in only 2% of feeding bouts (N = 109). Subordinate birds were frequently chased from carcasses; intruders and juveniles ended 38% (N = 65) and 47% (N = 85), respectively, of their feeding bouts at carcasses by being chased. Consequently, the mean durations of these feeding bouts at carcasses for territorial males (54 ± 80 sec, N = 65) and females (62 ± 63 sec, N = 109) were each significantly longer than those of intruders (37 ± 44 sec, N = 98) ($t = 1.74$, df = 161 and $t = 3.27$, df = 205, respectively, $P < 0.05$ in each case). The mean bout duration by juveniles (41 ± 46 sec, N = 131) was significantly less than that of females ($t = 2.98$, df = 238, $P < 0.05$), but was not significantly different from those of males ($t = 1.44$, df = 194, $P > 0.05$) or intruders ($t = 0.66$, df = 227, $P > 0.05$).

Most sheathbills swallowed few invertebrates and spent little time eating

them (Tables 3 and 4). The only significant differences here were that territorial females had lower swallowing rates than intruders. Although most territorial males ate few invertebrates, their mean eating time and intake of this food was boosted by two records in which males spent 79% and 95% of the eating time ingesting large kelp fly larvae taken from particularly productive patches of rotting kelp.

Most sheathbills ate some excreta, but generally only small amounts. Juveniles had higher rates of swallowing excreta than territorial females but there were no significant differences between other classes (Tables 3 and 4). Intruders and juveniles spent significantly more time eating and had higher rates of swallowing unidentified objects than territorial males and females (Tables 2 and 3). These unidentified objects were all very small and probably of low nutritional value.

The mean weight of juveniles trapped in King Penguin colonies during the winter (April through September) was 446 ± 74 g (N = 14), which was significantly higher (two-tailed *t*-test, $t = 1.90$, df = 67, $P = 0.05$) than the mean weight of juveniles trapped elsewhere in the same period (414 ± 50 g, N = 55). The minimum annual survival of juveniles banded in King Penguin colonies and those banded elsewhere was 0.55 (N = 14) and 0.33 (N = 59), respectively, over a two year period, 1974–1976. These data are presented tentatively since the disappearance of banded juveniles was due to death and also to movements to other parts of the island (Burger 1979).

DISCUSSION

The costs of territorial defense by sheathbills wintering in the King Penguin colony appeared to be low. Territorial adults spent less than 2% of their foraging time and similar low proportions of their overall daily time budget in overt chasing and threatening. There was also little risk of injury from fighting. Fighting occurred rarely, only between neighboring territorial adults and was seldom damaging (Burger 1980a, Burger and Millar 1980). The economical defense of territories was facilitated by conspicuous visual and vocal advertising (Burger 1980a), but there was no evidence that this conspicuousness might have increased the risk of predation by skuas. The sheathbills maintained the same territories with relatively stable boundaries from year to year (Burger 1980a), which probably facilitated their defense, as was found for some other species (Southern and Lowe 1968, Davies 1976).

Sheathbills appeared to benefit from winter territoriality in at least two ways, and possibly a third. Firstly, the territorial adults had greater access to high quality food than intruders. Very few non-territorial birds had the freedom from interference needed to stand waiting for opportunities

to kleptoparasitize penguins. Territorial adults were immediately dominant at penguin carcasses within their territories. They had longer feeding bouts at carcasses, with fewer interruptions, than the intruders did. Territorial females had significantly higher rates of swallowing carcass flesh than the intruders did. Territorial adults were undoubtedly very familiar with the food resources in their territories, which they crosssed many times a day. They spent more time eating and less walking in search of food than intruders.

The overall impression was that territorial adults had little difficulty in getting sufficient food, whereas the intruders had to spend more time and effort and quite frequently resorted to eating small items of low quality food. Despite this, many intruders appeared well fed, the King Penguin colonies attracted many non-territorial birds (Burger 1981a) and several banded individuals foraged as intruders all winter (Burger, unpubl. data 1974–1977).

Secondly, a territorial pair probably enhanced its inclusive fitness by permitting its offspring to overwinter in the territory. Juveniles were lighter than other birds (Burger 1980b), had higher rates of mortality than adults and were more commonly found dead and underweight following inclement weather (Burger 1979). Juveniles which foraged in King Penguin colonies were heavier in winter and appeared to have higher chances of survival than those elsewhere. Within their parents' territories they avoided much of the interference competition for food in these colonies. Juveniles were subjected to less chasing than intruders, although subordinate to those birds. Consequently, juveniles spent more time eating, with fewer interruptions, and less time walking than intruders.

Finally, adults which were territorial all winter were probably more likely to have retained their territories in King Penguin colonies at the onset of breeding than if they had abandoned them. I was unable to determine how many of the birds observed in 1978 subsequently bred in their territories but observations of color-banded birds in other years (1974–1977) showed that survivors always retained their territories in spring (Burger 1980a). At Marion Island, only the sheathbills with territories in penguin colonies bred, and some adults failed to obtain territories (Burger 1979), suggesting that there was competition for territories. Since King Penguin colonies generally attracted many sheathbills, it seems likely that the costs of re-establishing an abandoned territory there might exceed the cost of maintaining the territory all winter. Similar ideas have been suggested for other bird species (Fretwell and Lucas 1970, Pyke 1979). Snow (1956) showed that European Blackbirds which remained in their territories outside the breeding season were more likely to retain the territories.

Sheathbills which bred in Rockhopper Penguin colonies abandoned their territories in winter, but survivors always regained these territories, and their survival rates and breeding success were similar to those of adults from King Penguin colonies (Burger 1979, 1980a). Unlike King Penguin colonies, the Rockhopper Penguin colonies provided little food and attracted few sheathbills during winter (Burger 1981a). Nevertheless, adults began to re-occupy former territories there for several hours a day, several weeks before the Rockhopper Penguins arrived in the last week of October and there was once again a reliable food supply. By contrast, sheathbills in a King Penguin colony could maintain territories at this time while still getting sufficient food there.

It appeared that the cost of territorial behavior was low relative to the benefits which acrued to the territorial adults and their offspring. In general, territories are only economically defendable if the resources are predictable and spatially concentrated (Brown 1964, Brown and Orians 1970). During winter at Marion Island, only the King Penguin colonies met these requirements. Sheathbills foraging in other parts of the island in winter adopted other strategies, such as flocking (Burger 1982).

SUMMARY

Lesser Sheathbills (*Chionis minor*) were studied at Marion Island in the sub-Antarctic. During the winter non-breeding season, pairs defended their breeding territories in King Penguin colonies against adult and subadult intruders, but they permitted their juvenile offspring to forage within the territories. Adults defended the territories at apparently little cost and gained immediate benefits by having greater access to the high quality food than intruders. Their offspring also benefitted by avoiding much of the aggressive competition for food, and this probably enhanced their survival. Adults remaining in their territories might also have improved their chances of retaining the territories in the following breeding season, but this was not directly confirmed. Although intruders were chased frequently and had less access to superior food, the King Penguin colonies remained attractive foraging sites in winter for many sheathbills. Only at these colonies was the food supply predictable and concentrated to allow territoriality in winter.

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FISH DROPPED ON BREEDING COLONIES AS INDICATORS OF LEAST TERN FOOD HABITS

JONATHAN L. ATWOOD AND PAUL R. KELLY

Studies of seabird food habits are frequently based on stomach contents, direct observation of feedings performed at breeding colonies, or food remains contained in regurgitated or fecal pellets (Ashmole 1968, Pearson 1968, Lemmetyinen 1973, Nisbet 1973, Vermeer 1973, Ainley et al. 1981). However, some species neither regularly regurgitate food nor produce feces or pellets containing identifiable food remains and, in the study of small or threatened populations, collection of even limited numbers of individuals for analysis of stomach contents is precluded. Investigation of food habits in these cases requires either remote observation of feeding activities, which is often logistically difficult, or indirect, alternative approaches.

Although there has been considerable recent research on the breeding biology and population trends of the endangered California Least Tern (*Sterna antillarum browni*) (Massey 1974; Massey and Atwood 1978, 1981; California Department of Fish and Game, unpubl.) little has been published regarding its foraging ecology. Atwood and Minsky (1983) found that most feeding activity near three California breeding colonies occurred within 4 km of the sites in nearshore ocean waters; terns nesting at colonies located adjacent to viable estuarine areas appeared to feed mainly in marsh habitats. Massey (1974) found the diet of Least Terns in California to consist mostly of small fish, and others (Hardy 1957, Tompkins 1959, LeCroy 1976, Thompson 1982) have reported similar findings in various populations of this species and in its Old World counterpart, the Little Tern (*S. albifrons*) (Marples and Marples 1934, Meinertzhagen 1954, Schonert 1961, Dement'ev et al. 1969, Nadler 1976, Spaans 1978).

Swickard (1972) and Massey (1974) noted that various species of fish are often found on the ground in Least Tern breeding colonies in California, and suggested that such specimens may provide an indication of food eaten by adults and chicks. In this study we examine the relationship between the prey eaten by Least Terns and that dropped in the colonies, and use samples of dropped food items as indicators of inter-colony and year-to-year differences in the species' diet.

STUDY AREAS AND METHODS

Prey items dropped on 10 Least Tern breeding colonies were collected, identified and measured during the 1978–1983 nesting seasons (May–August); four colonies were repre-

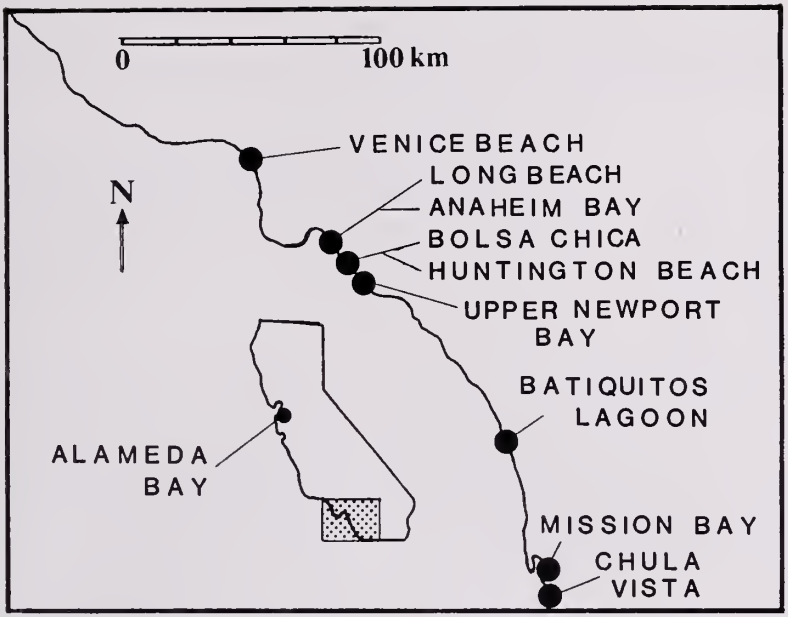

FIG. 1. Location of California Least Tern colonies represented by collections of fish dropped on substrate.

sented by samples obtained in at least two consecutive years. Colonies were distributed from the northern extreme of the Least Tern's California range south to the Mexican border (Fig. 1). Principal foraging habitats used by terns at different colonies varied somewhat, including: (1) nearshore ocean, harbors, and marina channels (Alameda Bay, Venice Beach, Long Beach, Huntington Beach), (2) tidal estuarine channels (Anaheim Bay, Bolsa Chica, Upper Newport Bay, Batiquitos Lagoon), and (3) sheltered, shallow bays (Mission Bay, Chula Vista).

To compare prey dropped and left in breeding colonies with food eaten by the terns, 131 feeding sequences between courting adults and 503 sequences involving adults feeding young were observed from May–July 1980 at colonies located at Venice Beach, Los Angeles County, and Huntington Beach, Orange County. Adult terns carrying prey were randomly selected as they approached a breeding colony and were observed until the food item had been transferred to another individual. The outcome of each feeding sequence was recorded in terms of whether the prey item was swallowed or dropped and left uneaten in the colony. Fish eaten during observed feedings were identified as to species whenever possible, and their body lengths placed in the following classes by comparison with the bill length of adult Least Terns: <2.5 cm; 2.5–5.0 cm; 5.0–7.5 cm; 7.5–10.0 cm. Prey items dropped and left uneaten at Venice Beach and Huntington Beach were collected during 1980 on 18 dates between 1 May and 20 June, and on 9 dates between 21 June and 1 August.

Clutch-size, shown to reflect variations in food availability in other *Sterna* spp. (Evans and McNicholl 1972, Nisbet 1973, Veen 1977), was monitored at Venice Beach during 1980–1983 and at Huntington Beach from 1981–1983. Only clutches initiated on or before 16 June were analyzed, thus eliminating from consideration the usually smaller clutches of

TABLE 1

COMPARISON OF FOOD EATEN BY LEAST TERNS WITH FISH LEFT UNEATEN AT VENICE BEACH AND HUNTINGTON BEACH BREEDING COLONIES, 1980

	% of fish observed eaten[a]				% of fish left uneaten on breeding colonies (N = 400)
	Courtship feedings (N = 130)	Small chick feedings (N = 107)	Large chick feedings (N = 392)	Total all feedings (N = 629)	
Northern anchovy/ silversides (spp.)	71	55	68	67	70
Unknown/miscellaneous slim-bodied spp.[b]	24	45	27	29	8
Surfperches (spp.)	4	—	3	3	9
Unknown/miscellaneous deep-bodied spp.	2	—	2	1	13

[a] Dates of observation: courtship feedings (15 May–25 May); small chick feedings (1–10 Jun.); large chick feedings (15 Jun.–25 Jul.).

[b] In columns referring to % fish observed eaten, this category includes mostly (>75%) unknown food items seen too poorly for specific identification. Northern anchovy and silversides (spp.) probably comprised a major portion of the unknown, slim-bodied fish observed to be eaten.

late-nesting individuals (Massey and Atwood 1981). Other possible indirect indicators of tern food availability, including frequency of egg abandonment, extent of non-predator related chick mortality and chick growth rates were also evaluated at these two colonies during 1980–1983; these data will be presented in detail elsewhere (Minsky, unpubl.; Collins and Atwood, unpubl.).

RESULTS

Observations of feeding sequences.—Small fish were the only prey item recorded during feeding sequences at Venice Beach and Huntington Beach in 1980, as well as during casual observations of Least Tern foraging activity in southern California during 1977–1983. We obtained no evidence that invertebrate prey represent an important portion of this population's diet during the nesting season.

Fish were rarely dropped in breeding colonies during feedings, with only 16 instances noted in 634 sequences. Fourteen of these 16 instances (87%) involved suitable food items that were dropped accidentally or as a result of lack of hunger on the part of the recipient. Five of these 16 dropped fish, 4 of which were suitable food items, were left uneaten on the ground, and 11 were retrieved and eaten after being dropped.

Although the size of prey eaten by Least Terns at Venice Beach and Huntington Beach in 1980 varied according to the feeding context, with small chicks receiving smaller food items than adults or juveniles, we obtained no indication that the composition of prey species changed significantly during the nesting season (Table 1). At least 67% of fish observed

TABLE 2
VARIATION IN CLUTCH-SIZE AT TWO LEAST TERN BREEDING COLONIES DURING 1980–1983

Colony	Year	N	Clutch-size			$\bar{x}$	SD
			1	2	3		
Venice Beach	1980	36	3	31	2	1.97	0.38
	1981	110	10	92	8	1.98	0.41
	1982	156	39	114	3	1.77[a]	0.50
	1983	128	10	113	5	1.96	0.34
Huntington Beach	1981	100	6	75	19	2.13	0.49
	1982	89	22	64	3	1.80[b]	0.51
	1983	77	5	58	14	2.12	0.49

[a] Significantly smaller (*t*-tests, $P < 0.05$) than 1980 ($t = 2.41$), 1981 ($t = 3.89$) and 1983 ($t = 4.22$) values.
[b] Significantly smaller (*t*-tests, $P < 0.05$) than 1981 ($t = 4.65$) and 1983 ($t = 4.16$) values.

to be eaten at Venice Beach and Huntington Beach in 1980 were northern anchovy (*Engraulis mordax*) or silversides (Atherinidae), and these species represented 70% of the specimens left uneaten at these colonies during the 1980 breeding season (Table 1). Surfperches represented 3% of fish observed eaten at Venice Beach and Huntington Beach in 1980, but 9% of the dropped prey items collected from these colonies; other "deep-bodied" species of fish were similarly over-represented in samples collected from breeding colonies relative to their occurrence as actual food items (Table 1).

Seventy-three percent of northern anchovies and silversides eaten by Least Terns of all age classes at Venice Beach and Huntington Beach in 1980 were <5.0 cm in length; in contrast, 87% of the individuals of these species dropped at these colonies were >5.0 cm in length. We observed no instances of northern anchovies or silversides being left uneaten on the substrate as a result of inappropriately large size per se; however, larger individuals of these species were frequently alive and struggling when transferred from parent to juvenile, and thus were more likely to be accidentally dropped. Over-representation in dropped fish collections of large northern anchovies and silversides relative to food actually eaten probably also reflects the increased chances of small dropped specimens being overlooked by investigators.

Analysis of food availability.—Least Tern food resources near Venice Beach and Huntington Beach were indirectly evaluated during 1980–1983. Mean clutch-size at both colonies during 1982 was significantly smaller than in 1980, 1981, and 1983 (Table 2). Similarly, significantly lowered asymptotic weights of chicks (Collins and Atwood, unpubl.) and increased levels of egg abandonment and non-predator related chick mor-

tality (Minsky, unpubl.) suggest conditions of low food availability near Venice Beach and Huntington Beach during 1982.

Collections of prey dropped in breeding colonies.—Major collections of fish dropped at 10 California Least Tern nesting areas during 1978–1983 are analyzed in Table 3. A total of 49 species of fish were found, all represented by individuals <1 year old. Most (59%) of the overall diversity resulted from the presence of 29 rarely encountered species that comprised only 3% of the total individuals collected (N = 3347). Northern anchovy and silversides (especially topsmelt [*Atherinops affinis*] and jacksmelt [*Atherinopsis californiensis*]) combined represented 67% of the total sample.

Thirty of 49 species of fish collected from nesting areas were represented primarily or entirely by individuals unsuitable as food items for Least Terns (Table 3); these species comprised 27% of the total individuals collected. General morphological characteristics of unsuitable prey species included preopercular or fin spines and/or maximum body depth or rotundity exceeding the gape width (approximately 1.5 cm as measured on fresh specimens) of adult Least Terns. Of deep-bodied species such as surfperches which were collected at Venice Beach and Huntington Beach in 1980, 89% of the individuals (N = 73) had maximum body depths >1.5 cm, and 38% were >2.0 cm. In contrast, "slim-bodied" species such as northern anchovy and silversides were represented mostly by individuals suitable as food items for Least Terns; 72% of these specimens collected at Venice Beach and Huntington Beach in 1980 (N = 351) had body depths <1.5 cm, and 100% were <2.0 cm.

Samples of fish dropped on various Least Tern breeding colonies showed significant inter-colony differences in the relative abundance of certain species (Table 3), apparently reflecting different feeding habitats and potential prey species available near each site. For example, terns at Venice Beach foraged primarily in nearshore ocean waters (Atwood and Minsky 1983) where schools of juvenile northern anchovy occurred (Fitch and Lavenberg 1971), and this species comprised up to 70% of the fish left uneaten at this colony. By contrast, terns breeding at Anaheim Bay fished mainly in shallow saltmarsh channels adjacent to the colony, where Klingbeil et al. (1975) found topsmelt and California killifish (*Fundulus parvipinnis*) to be common but northern anchovy and surfperches to be rare or absent during the summer months. Topsmelt and California killifish combined represented 82% of the fish dropped at Anaheim Bay in 1981, while northern anchovy and surfperches comprised only 7% of the sample. Samples of fish dropped at colonies located at Bolsa Chica and Batiquitos Lagoon, where terns similarly foraged mainly in tidal estuaries, were also dominated by topsmelt and California killifish rather than northern anchovy (Table 3). Deepbody (*Anchoa compressa*) and slough anchovies (*A.*

delicatissima), more southerly in distribution than the northern anchovy (Miller and Lea 1972), were the most abundant species dropped on colonies at the southern limit of the study area, but were rare or absent from sites farther north (Table 3).

Fish dropped in breeding colonies also showed significant year-to-year changes in species composition (Table 3), probably reflecting fluctuations in abundance or availability of those fish. In 1979, when large numbers of mosquitofish (*Gambusia affinis*) were stocked weekly in ponds adjacent to the Huntington Beach colony, the artificial population increase of this food species was clearly reflected by the increased occurrence of mosquitofish in samples of prey dropped on the adjacent breeding colony (Table 3). Similarly, the relative abundance of northern anchovy in samples of fish dropped at Venice Beach and Huntington Beach declined from 1978–1981 (Fig. 2), probably reflecting a documented decline during these years in the local availability of juveniles (<1 year old) of this important prey species (Methot 1982).

DISCUSSION

Collection of fish dropped on breeding colonies provides a simple way of monitoring Least Tern food habits at these sites. However, for the technique to be effective, a relationship must first be established between food items eaten by the terns and prey dropped and left uneaten on the nesting substrate.

Theoretically, if only suitable food items were dropped (due to surplus food and/or accident), samples of fish collected from the substrate would closely reflect prey eaten by terns at the breeding colony. If only unsuitable fish were left uneaten on the ground (because of difficulties in swallowing caused by inappropriately large size, spines or bad taste), samples would be poor indicators of actual food habits. Variations in the frequency with which suitable prey species were left uneaten on breeding colonies would be expected to crudely reflect overall food availability, since under poor food conditions not only would suitable prey items be captured less frequently by the terns, but those suitable fish which were brought to a colony would be "wasted" less often than when surplus food was present.

Palmer (1941) suggested that fish found dropped on Common Tern (*Sterna hirundo*) colonies were indicative of an abundant food supply, implying that many of the fish were surplus, but otherwise suitable, food items. However, he also noted that some fish had evidently been left uneaten as a result of excessively large size. Hulsman (1981:29) stated that "the width or depth of body of prey often limits the size of prey eaten (by terns) before its length does"; Courtney and Blokpoel (1980) found that although deep-bodied or rotund species were over-represented,

TABLE 3

RELATIVE ABUNDANCES OF FISH DROPPED ON CALIFORNIA LEAST TERN BREEDING COLONIES, 1978–1983

Species[b]	Breeding colony and year[a]																				
	AL	VB						LB			AB		BC	HB				NB	BL	MB	CV
	81	78	79	80	81	82	83	78	79	81	80	81	81	79	80	81	82	78	81	81	81
Clupeidae																					
Dorosoma petenense	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–
**Clupea harengus*	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Engraulidae																					
**Engraulis mordax*	11	70	53	47	28	17	65	60	33	25	2	5	5	59	41	19	13	71	13	22	8
**Anchoa compressa*	–	–	–	–	–	1	–	2	11	–	–	2	–	+	–	–	2	–	–	–	1
**A. delicatissima*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
**A. compressa*/ *A. delicatissima*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	43	27
Salmonidae																					
**Oncorhynchus tshawtscha*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Osmeridae																					
**Hypomesus transpacificus*	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hemiramphidae																					
Hyporhamphus rosae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
Belonidae																					
Strongylura exilis	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
Scomberesocidae																					
Cololabis saira	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyprinodontidae																					
Fundulus parvipinnis	–	1	2	2	3	5	–	2	–	–	22	16	17	+	1	3	–	–	7	6	8

TABLE 3
CONTINUED

Species[b]	Breeding colony and year[a]																				
	AL	VB						LB			AB		BC	HB				NB	BL	MB	CV
	81	78	79	80	81	82	83	78	79	81	80	81	81	79	80	81	82	78	81	81	81
Atherinidae																					
**Leuresthes tenuis*	–	?	–	2	1	?	1	?	–	–	–	–	1	–	1	1	?	?	–	–	–
**Atherinopsis californiensis*	47	?	4	5	11	?	?	?	4	–	2	–	–	6	9	12	?	?	–	–	–
**Atherinops affinis*	7	?	16	17	16	?	?	?	4	42	52	64	42	14	12	37	?	?	78	25	19
*Atherinidae (spp.)	–	15	–	–	5	24	14	15	–	–	17	–	–	–	4	–	31	19	–	–	–
Gasterosteidae																					
Gasterosteus aculeatus	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Centriscidae																					
Macrorhamphosus gracilis	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Scorpaenidae																					
Sebastes serriceps	–	–	+	+	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. paucispinis	–	–	+	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
S. spp.	–	1	+	5	1	2	1	–	–	–	–	–	–	+	12	1	2	–	–	–	–
Anoplomatidae																					
**Anoplopoma fimbria*	–	–	–	+	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Hexagrammidae																					
**Hexagrammos decagrammus*	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cottidae																					
Scorpaenichthyes marmoratus	–	1	+	2	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leptocottus armatus	–	–	1	–	–	–	–	–	4	–	–	–	–	–	2	–	–	–	–	–	–

TABLE 3
CONTINUED

Species[b]	Breeding colony and year[a]																				
	AL	VB						LB			AB		BC	HB				NB	BL	MB	CV
	81	78	79	80	81	82	83	78	79	81	80	81	81	79	80	81	82	78	81	81	81
Carangidae																					
Trachurus symmetricus	–	–	–	–	+	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Pristipomatidae																					
Anisotremus davidsonii	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sciaenidae																					
**Seriphus politus*	–	–	–	–	+	1	–	–	–	–	–	–	–	+	–	–	–	–	–	2	–
Genyonemus lineatus	–	–	–	–	+	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Girellidae																					
Girella nigricans	–	–	+	–	16	2	1	–	–	–	–	1	–	–	–	2	2	–	–	–	–
Scorpididae																					
Medialuna californiensis	–	2	–	–	–	–	–	–	–	–	–	–	–	1	–	+	–	–	–	–	1
Embiotocidae																					
Amphistichus argenteus	–	–	–	–	+	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–
Hyperprosopon argenteum	1	1	4	4	2	7	2	24	7	–	–	–	–	5	2	–	6	–	–	–	–
Cymatogaster aggregata	16	5	7	7	2	5	4	–	15	17	–	2	1	13	2	17	42	9	2	–	9
Micrometrus minimus	–	+	5	1	4	2	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Phanerodon furcatus	3	2	4	–	–	1	–	–	22	–	–	–	–	+	–	–	–	–	–	–	–
Embiotocidae (spp.)	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pomacentridae																					
Chromis punctipinnis	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 3
CONTINUED

Species[b]	Breeding colony and year[a]																				
	AL	VB						LB			AB		BC	HB				NB	BL	MB	CV
	81	78	79	80	81	82	83	78	79	81	80	81	81	79	80	81	82	78	81	81	81
Sphyraenidae																					
**Sphyraena argentea*	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Clinidae																					
Heterostichus rostratus	–	–	–	–	+	1	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–
Gobiidae																					
**Gillichthys mirabilis*	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	2	9
Acanthogobius flavimanus	1	–	2	5	2	1	2	–	–	4	–	8	–	–	–	1	–	–	–	–	–
**Clevelandia ios*	–	+	–	–	+	–	1	–	–	–	–	–	8	–	–	–	–	–	–	–	3
**Quietula y-cauda*	–	1	–	–	2	29	6	–	–	–	5	–	3	–	–	+	2	–	–	–	12
Scombridae																					
Scomber japonicus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Centrolophidae																					
**Icichthys lockingtoni*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stromateidae																					
Peprilus simillimus	–	–	–	+	+	+	1	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Centrachidae																					
Lepomis sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–
Poecilidae																					
**Gambusia affinis*	–	–	–	–	+	–	–	–	–	–	–	–	–	12	1	2	–	–	–	2	–

TABLE 3
CONTINUED

Species[b]	Breeding colony and year[a]																				
	AL	VB						LB			AB		BC	HB				NB	BL	MB	CV
	81	78	79	80	81	82	83	78	79	81	80	81	81	79	80	81	82	78	81	81	81
Cichlidae																					
Tilapia sp.	—	—	—	—	—	—	—	—	—	—	—	—	21	2	3	—	—	—	—	—	—
Cyprinidae																					
Cyprinus carpio	—	—	—	—	—	—	—	—	—	—	—	—	1	2	2	—	—	—	—	—	—
**Notemigonus crysoleucas*	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sample size (N)	73	379	267	230	545	181	123	126	27	24	102	91	118	250	170	312	48	66	46	63	106

[a] Percentage of each year's total sample (N) is provided; (+) = value less than 1%, (?) = species included in more general category of identification such as Atherinidae (spp.). Colony abbreviations as follows: AL = Alameda Bay, VB = Venice Beach, LB = Long Beach, AB = Anaheim Bay, BC = Bolsa Chica, HB = Huntington Beach, NB = Upper Newport Bay, BL = Batiquitos Lagoon, MB = Mission Bay, CV = Chula Vista.

[b] Family and species names based on Miller and Lea (1972).

* Species represented mostly (>50%) or entirely by individuals considered to be suitable food items for Least Terns.

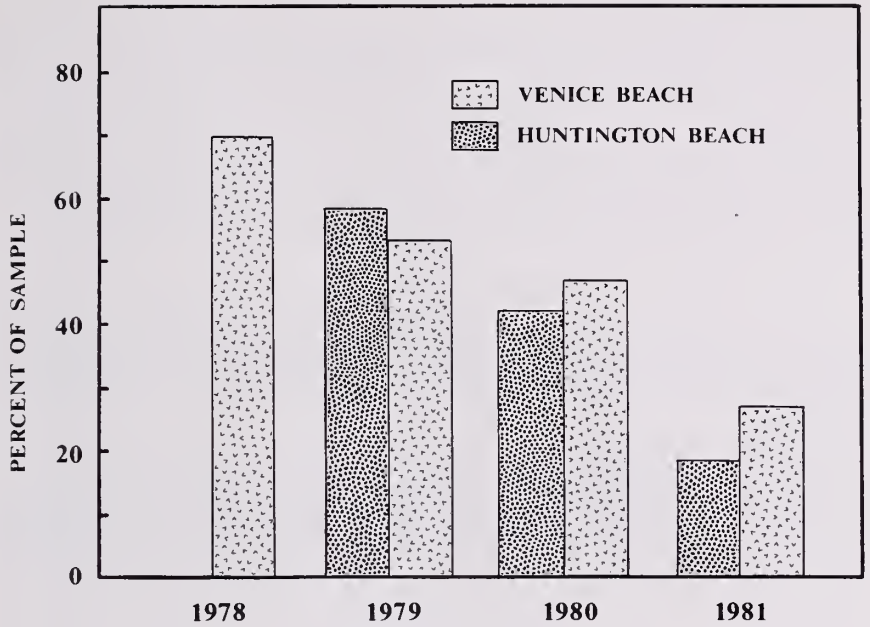

FIG. 2. Relative abundance of northern anchovy in collections of fish dropped at two study colonies.

samples of fish dropped in nesting areas accurately reflected the principal prey species eaten by Common Terns.

Collections of prey dropped by Least Terns appeared to correctly indicate the principal fish species eaten at breeding colonies in this study; however, various biases made samples of dropped fish inaccurate indicators of the size of prey eaten. Although unsuitable (especially deep-bodied) prey species were over-represented in collections of dropped fish relative to their use in observed feedings, in all cases samples obtained at the colonies were composed of primarily suitable food items that probably had been dropped as a result of accident or lack of hunger.

Northern anchovy was the dominant prey species in nine samples, silversides (especially topsmelt and jacksmelt) in seven, and deepbody or slough anchovies in two. These species appear to be the main food items eaten by Least Terns at California breeding colonies. This conclusion is consistent with an analysis of 11 stomach contents obtained from adult and juvenile Least Terns found dead in southern California (Kelly, unpubl.).

The relative abundance of the principal prey species in collections of dropped fish generally reflected overall food conditions in the vicinities

of breeding colonies. During 1980, 1981, and 1983, 61–70% of fish left uneaten at Venice Beach and Huntington Beach were northern anchovies and silversides, which were determined by observation to be the dominant prey species eaten at these sites. In 1982, however, when smaller clutch-sizes, reduced asymptotic weights of chicks, and increased levels of egg abandonment and nonpredator related chick mortality indicated unusually low food availability near these colonies, northern anchovy and silversides comprised only 41% of the fish left uneaten on these sites.

SUMMARY

Samples of fish dropped at 10 Least Tern breeding colonies were, in general, valid indicators of the principal prey species being eaten at a colony. Collection of such specimens provides a simple means of crudely monitoring year-to-year and inter-colony differences in feeding habits.

Northern anchovy, topsmelt, jacksmelt, and deepbody or slough anchovies were the primary food items eaten by Least Terns in California. In 1982, when smaller mean clutch-sizes, lowered asymptotic chick weights, and increased levels of egg abandonment and nonpredator related chick mortality indicated conditions of low food availability near two study colonies, the dominant prey species eaten at these sites were dropped in the colonies less frequently than during 1980, 1981, and 1983.

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RELATIONSHIP OF BREEDING BIRD DENSITY AND DIVERSITY TO HABITAT VARIABLES IN FORESTED WETLANDS

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Richard M. DeGraaf

Deciduous forested wetlands are defined as lands dominated by deciduous trees where the water table is at, near, or above the land surface long enough each year to promote the formation of hydric soils, and to support the growth of hydrophytes (Cowardin et al. 1980). This wetland type comprises more than half (75,000 ha) of the total freshwater wetland area in Massachusetts (Golet and Larson 1974) and is common throughout the northeastern U.S.

This study relates breeding bird density and species richness to habitat features in forested wetlands. The basis for relating avian distribution to habitat variables is an hypothesis that physical features may ultimately reflect the suitability of a site for reproduction and survival (Hilden 1965). The distribution and abundance of breeding birds has been related to habitat features in a variety of upland forest types (Anderson and Shugart 1974, Bond 1957, James 1971, Odum 1950, Shugart and James 1973, Smith 1977, and various authors in Smith 1975 and DeGraaf 1978). There has been, however, limited documentation of breeding bird habitat relationships in wetland forest communities, where surface hydrology is a dominant feature affecting the plant and animal community.

METHODS

Study areas.—This research was conducted in eight deciduous forested wetlands, each 30 ha or larger, in the southern half of the Connecticut Valley region of Massachusetts (Fig. 1). Study areas were selected to provide a wide range of vegetation structure, hydrologic patterns, and geographic location.

Quinebaug Swamp was predominantly a shrub swamp with widely spaced young trees in the overstory. Lawrence Swamp and Leadmine Swamp were patchy woodlands with dense stands of sapling to pole-sized trees, mature forest and brushy openings along streams. The other five study areas were more homogeneous, early to late stages of mature red maple forest.

Red maple (*Acer rubrum*) was the most abundant tree species in the overstory of all study areas. American elm (*Ulmus americanus*), yellow birch (*Betula alleghaniensis*), black ash (*Fraxinus nigra*), hemlock (*Tsuga canadensis*), and black gum (*Nyssa sylvatica*) were much less abundant in the canopy layer, but were frequent in young forest stands and as subcanopy trees in mature stands. Several areas had small "islands" of slightly higher elevation occupied by white oak (*Quercus alba*) and white pine (*Pinus strobus*), but these islands were

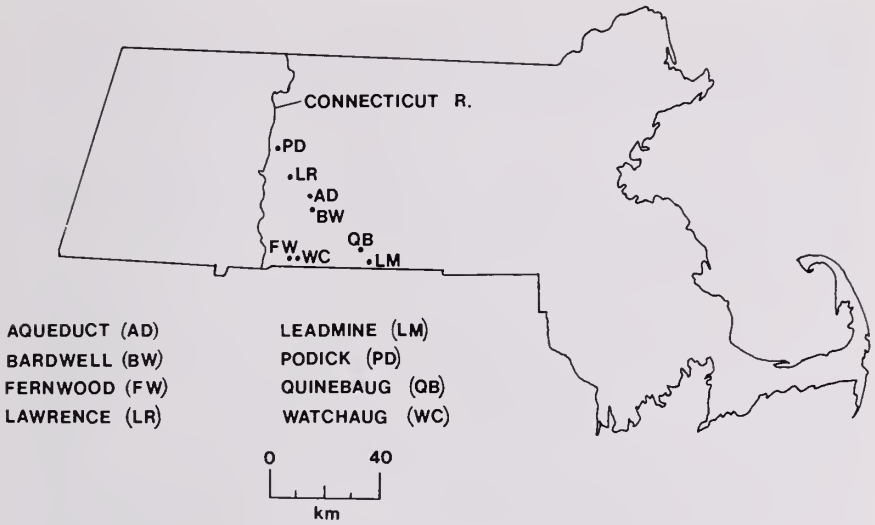

FIG. 1. Names and locations of deciduous forested wetland study areas, Massachusetts.

generally avoided in the selection of census plot locations. Woody plants common in the understory included common winterberry (*Ilex verticillata*), highbush blueberry (*Vaccinium corymbosum*), alder (*Alnus* spp.), arrow-wood (*Viburnum dentatum*), spicebush (*Lindera benzoin*), silky dogwood (*Cornus amomum*), swamp-rose (*Rosa palustris*) and spiraea (*Spiraea* spp.). Cinnamon fern (*Osmunda cinnamonea*), royal fern (*Osmunda regalis*), hummock sedge (*Carex stricta*), skunk cabbage (*Symplocarpus foetidus*), poison ivy (*Toxicodendron radicans*), and sphagnum moss (*Sphagnum* spp.) were common in the herbaceous layer.

Shallow pools of surface water were present on portions of all sites in late May, but disappeared from many during the summer. All study areas showed a seasonal pattern of high water levels in early spring with a drawdown normally occurring into September, depending on rainfall. In 1978, water levels returned to near spring levels by December, exhibiting the annual cycle described by Lyford (1964) for wet forested soils in New England. Plots within each wetland exhibited similar patterns of fluctuation, but range of water table fluctuation was variable among and within most study areas (Swift 1980).

Bird populations.—Data on breeding bird populations were collected on 10 circular 0.25-ha plots (28.2-m radius) within each study area. All plot centers were located at least 100 m from any border with non-hardwood forest cover. Birds were censused on each plot six times per year between 31 May and 30 June, in both 1978 and 1979, between 05:00 and 09:00 EST (when there was no precipitation or strong winds). Each census consisted of a 5-min listening period at a plot center, during which all singing male birds were identified to species and counted. Relative abundance of each species was determined for each plot based on the mean number of singing males observed.

Bird census data were compiled to produce five avian community variables. Total breeding bird density (TBD) was the sum of the relative abundances of all species on a plot. Bird species richness (BSR) was the total number of species observed on a plot during the two

breeding seasons. Most species were placed into one of three primary feeding guilds (after Holmes et al. 1979): ground and herb foragers (GRGILD), foilage gleaning birds (FLGILD), and trunk and branch (bark) foragers (BKGILD). The number of birds in each guild was the sum of the relative abundances of the appropriate species. Grouping into guilds was done to identify important habitat components for birds sharing a common foraging substrate.

Habitat measurements.—Analysis of avian habitats was based on measurement and estimation of 15 physical aspects of vegetation and hydrology (moisture regime) at each census plot. Habitat variables included in the study and methods used to measure each are described below. Abbreviations for variables are indicated in parentheses.

Vegetation sampling was conducted on a 0.02-ha area within each census plot during July and August 1978. The sampled area was defined by two perpendicular, rectangular transects (51 × 2 m each), intersecting at the plot center, and oriented in the cardinal directions. Stem counts were divided into size classes as follows: live overstory trees, dbh > 7.7 cm (TREE); subcanopy stems > 5 m in height and dbh ≤ 7.7 cm (SUBCAN); shrub stems 3–5 m in height and dbh ≤ 7.7 cm (TALL); shrub stems 1–3 m in height and dbh ≤ 7.7 cm (SHORT); and standing dead trees, dbh > 7.7 cm (DEAD). Heights of overstory trees were estimated from clinometer readings to determine average height of trees (AVGHGT) and height of the tallest tree (MAXHGT) in the sampled area. Percent crown closure (CROWN) and percent herbaceous cover (HERB) were estimated by noting presence or absence of vegetation in the respective layers at 20 locations along transect center lines. Other vegetation variables were average dbh of overstory trees (DBH) and average height above ground of the lowest live branches on overstory trees (BOLE).

Percent surface "wetness" (WET) was estimated by visually noting presence or absence of surface water at 64 points along the transect center lines. This was done in early June 1978. Presence of streams (STREAM) on plots was noted, and included any channel of flowing water, regardless of size or rate of flow. Depth of muck (SOIL) was measured at all plots by probing with a 0.5 in diameter iron rod to depth of refusal (i.e., where dense mineral soil resisted further penetration), down to a maximum of 2.4 m. This parameter may reflect soil drainage characteristics, since muck soils generally have low vertical permeability (O'Brien 1977).

Water levels were monitored within wells (1.0 m depth × 0.1 m diameter perforated plastic pipe, after Lyford 1964) installed at the center of five census plots in each study area. Measurements were taken concurrently with bird censuses in June 1978 and 1979. During the remainder of the year, data were collected at 4–6 week intervals; all wells were visited within a 36-h period following a minimum of 48 h without precipitation. The magnitude of observed water level fluctuation, i.e., the vertical distance between maximum and minimum recorded water levels (FLUX), was determined for each well. Values for this variable were not estimated for plots that were not monitored.

Quantitative analyses.—Relationships between the five avian community parameters and habitat variables were assessed by multiple regression (ordinary least squares) and simple correlation (Johnston 1972). Data from all plots were used to produce a multiple regression model for each avian community variable. No transformations of data were applied. Water level fluctuation (FLUX) was not included as a habitat variable in the multiple regressions because data were collected from only half of the census plots. Multicollinearity among habitat variables was assessed using additional multiple regressions referred to as "auxiliary regressions" (Johnston 1972). In all analyses, Student's t-test ($P \leq 0.05$) was used to determine significance of the regression coefficient for each habitat variable. F-tests were used to assess the ability of each multiple regression to explain variation of the particular dependent variable.

RESULTS

A total of 2679 observations of singing male birds were recorded, comprising 46 species (Swift 1980). Overall, the most common species were: Common Yellowthroat (*Geothlypis trichas*), Veery (*Catharus fuscescens*), Canada Warbler (*Wilsonia canadensis*), Ovenbird (*Seiurus aurocapillus*), Northern Waterthrush (*S. noveboracensis*), Gray Catbird (*Dumetella carolinensis*), and Black and White Warbler (*Mniotilta varia*). These species accounted for 72% of the observations. While species compositions of study areas were similar, relative abundances and total breeding bird densities were variable.

Estimated densities of birds in the study areas ranged from approximately 132 ± 80 (SD) to 720 ± 113 males per 40 ha (Table 1). Mean density of birds for all areas was 446 ± 195 breeding males per 40 ha. Overall, foliage gleaning birds were the most abundant feeding guild (221 ± 128 males/40 ha), followed by ground feeders (168 ± 88 males/40 ha) and bark gleaners (49 ± 42 males/40 ha). Total number of species observed in the study areas ranged from 15–22, while the mean number of species per plot ranged from 5.5 ± 2.5–10.8 ± 1.9 among study areas.

There were marked differences in habitat characteristics among and within study areas (Table 2). A significant amount of variation in total breeding bird density (TBD), bird species richness (BSR), and abundance of birds in two of the feeding guilds (FLGILD and GRGILD) was explained by habitat variables (Table 3). TBD was positively correlated with small shrub density, surface wetness, and soil depth. BSR was also positively correlated with small shrub density and soil depth, and was inversely related to tall shrub density and height of lowest branches. FLGILD was positively related to surface wetness and soil depth, and was inversely related to percent crown closure. GRGILD was positively related to number of dead trees. No significant results were obtained in the model for bark-foraging species. Extreme multicollinearity was apparent for seven habitat variables which had R^2's > 0.70 (Table 2). This may have precluded the detection of other significant habitat relationships in the multiple regression models.

Results of simple correlations between the avian community parameters and all habitat variables are presented in Table 4. Magnitude of water level fluctuation (FLUX), which ranged from 4–86+ cm, was more highly correlated to TBD, BSR, and FLGILD than was any other habitat variable.

DISCUSSION

Densities and species' richness of breeding birds in this study were generally comparable to those observed in other moist woodlands, such as

TABLE 1

SUMMARY OF BREEDING BIRD CENSUS RESULTS ($\bar{x} \pm$ SD) FOR EIGHT DECIDUOUS FORESTED WETLANDS

Avian variable[a]	Study area[b]								
	AD	BW	FW	LR	LM	PD	QB	WC	ALL
TBD (obs./plot/year)[c]	15.95 ±4.03	14.95 ±3.73	18.05 ±7.43	20.10 ±3.36	19.75 ±2.26	4.95 ±2.99	26.95 ±4.25	13.05 ±4.83	16.72 ±7.29
FLGILD (obs./plot/year)	8.25 ±3.36	5.30 ±2.57	8.05 ±2.82	11.80 ±3.34	10.75 ±1.85	2.00 ±1.24	14.05 ±3.97	5.90 ±4.62	8.26 ±4.81
GRGILD (obs./plot/year)	5.55 ±2.92	6.90 ±1.89	6.05 ±3.78	7.45 ±1.17	5.70 ±1.69	2.30 ±1.27	11.15 ±2.26	5.35 ±2.70	6.31 ±3.31
BKGILD (obs./plot/year)	2.10 ±1.32	2.30 ±1.35	3.55 ±1.80	0.75 ±0.60	3.05 ±1.23	0.35 ±0.59	1.10 ±1.04	1.50 ±0.89	1.84 ±1.57
BSR (no. species/plot)	9.70 ±2.36	8.00 ±2.05	10.60 ±2.95	9.00 ±2.00	9.90 ±0.99	5.50 ±2.46	10.80 ±1.87	8.60 ±1.84	9.00 ±2.60
Total no. species/area	22	19	21	21	18	15	19	22	46

[a] Abbreviations explained in text.
[b] Study area abbreviations explained in Fig. 1.
[c] Density per 40 ha can be computed by multiplying the value by 26.7.

riparian communities, wooded swamps, and cove forests (Brinson et al. 1981). However, the observed significant differences in density and diversity among study areas were not anticipated. This provided an opportunity to closely examine habitat relationships to avian communities in deciduous forested wetlands.

Results of the multiple regressions support an hypothesis that vegetation structure had a significant effect on breeding bird communities in forested wetlands. For example, an increase in number of small shrubs (1–3 m in height) was associated with an increase in both breeding bird density and species richness. The addition of shrubs to the understory would increase structural heterogeneity in a forest, which is believed to be important for providing avian niche diversity (MacArthur and MacArthur 1961, Roth 1976). At the same time, however, the number of tall shrubs (3–5 m) was inversely related to bird species richness. This may suggest that the taller shrubs occupied open space and vertical "edges" that would otherwise have existed between the understory and canopy layers of vegetation; this could affect foraging maneuverability of birds (Balda 1975). The relationship of crown closure to BSR also suggests that openings in the canopy, which would increase structural heterogeneity, enhanced diversity of the bird community. From the data available, it was not possible to hypothesize whether the vegetation variables also reflected differences in site productivity or foliage volume, which have been suggested as possible factors affecting breeding bird communities (Lack 1966, Cody 1974, Willson 1974, Gauthreaux 1978).

Significant correlations were found between the avian community parameters and variables used to quantify hydrologic conditions. These observations may indicate that moisture regime is a basic habitat feature affecting breeding bird communities in forested wetlands. In this study, percent surface wetness and depth of muck were directly related to avian density and species' richness. It appears that the most poorly drained sites had the most abundant and diverse bird populations. This hypothesis was further supported by the inverse correlation between magnitude of water level fluctuation and avian density and species' richness.

The apparent relationship of breeding bird density and diversity to moisture regime may be due to greater understory vegetation and more diverse vegetative structures found in mesic sites (Curtis and Ripley 1975, Dickson 1978). Data collected in this study indicated that percent surface wetness was positively correlated with shrub and subcanopy stem densities (Swift 1980). However, not all moist sites produce a well developed understory. Abundance of understory vegetation in wetland forests may be adversely affected by fluctuating water levels (M. M. Brinson, pers. comm.; Flinchum 1977). In this study, magnitude of water level fluctuation had

TABLE 2

SUMMARY ($\bar{x}$ ± SD) OF HABITAT MEASUREMENTS FOR EIGHT DECIDUOUS FORESTED WETLANDS

Habitat variable[a]	Study area[b]									
	AD	BW	FW	LR	LM	PD	QB	WC	ALL	$(R^2)^c$
TREE (no./plot)	13.6 ±6.7	11.6 ±4.5	14.6 ±5.4	15.6 ±5.9	21.3 ±7.5	13.7 ±5.0	11.3 ±5.2	18.5 ±6.5	15.0 ±6.7	0.42
SUBCAN (no./plot)	1.7 ±2.4	1.8 ±2.6	4.2 ±3.1	16.8 ±7.9	9.2 ±6.8	2.6 ±2.2	10.9 ±5.3	2.3 ±3.1	6.2 ±7.0	0.58
TALL (no./plot)	5.7 ±3.9	11.6 ±23.9	11.8 ±5.4	52.1 ±29.1	25.5 ±19.1	4.2 ±3.0	67.4 ±21.3	5.2 ±4.7	22.9 ±28.2	0.82
SHORT (no./plot)	143.1 ±90.9	155.2 ±123.8	165.7 ±64.5	419.1 ±113.5	263.8 ±155.2	67.9 ±23.0	605.9 ±169.6	166.8 ±57.8	248.4 ±200.1	0.87
DEAD (no./plot)	2.6 ±2.7	2.5 ±2.3	4.2 ±2.3	1.0 ±0.9	2.3 ±1.7	2.3 ±2.0	1.5 ±1.3	3.5 ±1.4	2.5 ±2.1	0.26
AVGHGT (m)	14.0 ±2.0	15.6 ±2.3	13.9 ±2.4	10.6 ±1.0	11.9 ±1.5	15.4 ±1.9	7.9 ±1.0	12.9 ±1.3	12.8 ±3.0	0.91
MAXHGT (m)	18.9 ±1.6	19.7 ±2.0	21.1 ±1.4	14.3 ±2.0	16.3 ±2.0	21.9 ±1.9	10.3 ±1.4	17.8 ±2.0	17.5 ±4.0	0.83
BOLE (m)	4.4 ±0.9	5.1 ±1.2	4.9 ±1.2	3.9 ±0.7	5.1 ±0.8	6.1 ±0.8	2.7 ±0.5	4.1 ±0.6	4.5 ±1.3	0.64
DBH (cm)	20.0 ±4.7	21.9 ±4.5	20.3 ±4.3	13.2 ±1.8	15.8 ±2.9	19.0 ±3.4	12.9 ±1.6	18.3 ±3.5	17.7 ±4.7	0.81
CROWN (%)	87.0 ±12.1	94.5 ±4.7	86.0 ±9.4	59.5 ±18.5	83.0 ±12.5	86.0 ±8.0	59.0 ±18.1	94.0 ±3.0	81.1 ±17.8	0.72
HERB (%)	80.5 ±7.9	69.0 ±13.8	79.0 ±10.2	77.0 ±15.4	78.0 ±15.0	74.0 ±14.8	80.5 ±8.2	80.5 ±12.3	77.3 ±13.1	0.20

TABLE 2
CONTINUED

Habitat variable[a]	Study area[b]									
	AD	BW	FW	LR	LM	PD	QB	WC	ALL	$(R^2)^c$
WET (%)	29.0 ±27.2	46.6 ±19.9	33.9 ±19.6	59.5 ±10.5	53.0 ±12.1	0.6 ±1.8	65.5 ±7.4	47.8 ±14.5	42.0 ±25.1	0.54
STREAM (1/0)	0.0 ±0.0	0.0 ±0.0	0.3 ±0.5	0.5 ±0.5	0.4 ±0.5	0.0 ±0.0	0.1 ±0.3	0.2 ±0.4	0.2 ±0.4	0.24
SOIL (cm)	193.9 ±73.9	93.4 ±56.0	170.7 ±32.3	89.6 ±53.4	200.6 ±48.4	41.0 ±8.3	182.8 ±37.2	138.6 ±82.4	138.8 ±76.6	0.36
FLUX (cm)	38.0 ±5.7	40.4 ±14.8	30.2 ±8.7	33.6 ±16.6	9.2 ±3.7	71.0 ±15.0	8.2 ±2.6	34.8 ±14.8	33.2 ±21.4	0.83

[a] Abbreviations explained in text.
[b] Abbreviations explained in Fig. 1.
[c] Values of R^2 are for the auxiliary regressions relating each habitat variable to all others except FLUX.

TABLE 3

RELATIONSHIPS BETWEEN AVIAN PARAMETERS AND HABITAT VARIABLES DETERMINED BY MULTIPLE REGRESSIONS[a]

Habitat variable	Avian community variables				
	TBD	BSR	FLGILD	GRGILD	BKGILD
Constant	10.270	4.531	5.661	7.083	−1.667
TREE	−0.057	−0.061	0.036	−0.054	−0.016
SUBCAN	−0.026	0.031	0.007	0.001	−0.026
TALL	−0.017	−0.040*	−0.023	−0.005	0.006
SHORT	0.017*	0.007*	0.008	0.008	0.000
DEAD	0.497	0.025	−0.068	0.427*	0.132
AVGHGT	0.791	0.431	0.600	0.119	0.035
MAXHGT	−0.294	0.037	−0.153	0.174	0.029
BOLE	−1.043	−0.747*	−0.276	0.675	−0.062
DBH	0.063	−0.047	−0.650	0.112	0.039
CROWN	−0.080	0.014	−0.108**	−0.001	0.016
HERB	0.008	0.011	0.020	−0.013	−0.001
WET	0.065*	0.012	0.620**	0.005	0.010
STREAM	2.862	1.159	1.529	0.267	0.775
SOIL	0.027**	0.014**	0.018**	0.007	0.002
R^2	0.70**	0.46**	0.72**	0.47**	0.18

[a] Values in the table are multiple regression coefficients for effects of habitat variables, and respective R^2's for the model of each avian variable. Significance levels indicated as follows: * ($P \leq 0.05$); ** ($P \leq 0.01$); df = 66.

a significant inverse correlation with abundance of small shrub stems ($r = -0.64$), tall shrub stems ($r = -0.58$), and subcanopy stems ($r = -0.42$).

The effects of hydrologic patterns on breeding birds in forested wetlands may be greater than the potential influence on vegetation structure. Smith (1977) documented the association of several bird species to vegetation components that corresponded to a more basic preference for positions on the moisture gradient of a forest. In this study, percent surface wetness and depth of muck had significant relationships to avian community variables that were not accounted for by vegetation variables in the multiple regressions. That is, if the vegetation variables remained constant, an increase in breeding bird density (especially foliage gleaners) and species' richness would be expected at sites with deeper organic soils and greater coverage by seasonal surface water. The explanation for these relationships was not determined.

Odum (1950) speculated that higher water content of forests could result in increased bird populations, both directly by providing more available water and moderating temperature changes, and indirectly by producing a more luxuriant vegetation, with greater variety of niches, and perhaps

TABLE 4

SIMPLE CORRELATIONS (*r*) BETWEEN AVIAN COMMUNITY PARAMETERS AND HABITAT VARIABLES[a]

Habitat variable	TBD	BSR	FLGILD	GRGILD	BKGILD
TREE	−0.16	−0.11	−0.02	−0.18	0.04
SUBCAN	0.10	0.31**	0.40**	0.21	−0.22
TALL	0.19	0.57**	0.59**	0.46**	−0.19
SHORT	0.36**	0.68**	0.68**	0.56**	−0.17
DEAD	0.08	0.07	0.21	0.02	0.26*
AVGHGT	−0.23*	−0.52**	−0.53**	−0.45**	0.18
MAXHGT	−0.28*	−0.60**	−0.63**	−0.48**	0.19
BOLE	−0.37**	−0.53**	−0.46**	−0.51**	0.10
DBH	−0.05	−0.31**	−0.39**	−0.20	0.20
CROWN	−0.28*	−0.56**	−0.63**	−0.40**	0.23*
HERB	0.20	0.15	0.17	0.08	−0.01
WET	0.29*	0.57**	0.61**	0.34**	0.03
STREAM	0.27*	0.33**	0.37**	0.12	0.08
SOIL	0.43**	0.45**	0.41**	0.31**	0.16
FLUX[b]	−0.46**	−0.80**	−0.75**	−0.43**	−0.22

[a] Significance levels indicated as follows: * ($P \leq 0.05$); ** ($P \leq 0.01$), df = 78.
[b] df = 38.

a greater amount of food. It is also possible that moisture conditions affect reproduction or distribution of plants and invertebrates (Gaines 1974, Brown et al. 1978), resulting in differences in food availability among structurally similar plant communities. However, these parameters were not analyzed in this study.

Conclusions.—Deciduous forested wetlands appear to be productive habitats for breeding birds. Although forested wetlands usually share a common assemblage of species, total bird density, species' richness and foraging guild structure are significantly affected by components of vegetation structure and hydrology. Analyses of breeding bird habitats should include efforts to quantify and explain the potential effects of moisture regime.

SUMMARY

Breeding bird populations were studied in eight deciduous forested wetlands located in the Connecticut Valley region of Massachusetts. Singing male birds were counted on 10 circular 0.25-ha plots in each study area in June 1978 and 1979. A total of 46 species was observed, with estimated densities varying among study areas from 134–720 males per 40 ha. Avian community parameters (total breeding bird density, bird species richness, and abundance of three foraging guilds) were related to 15 habitat variables by multiple regression

and simple correlation. Results suggested that breeding bird communities in forested wetlands are significantly related to vegetation structure and hydrology. Generally, the most poorly drained sites appeared to have the most abundant and diverse breeding bird populations.

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A COMPARISON OF BREEDING ECOLOGY AND REPRODUCTIVE SUCCESS BETWEEN MORPHS OF THE WHITE-THROATED SPARROW

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The White-throated Sparrow (*Zonotrichia albicollis*) is polymorphic in plumage and behavior (Lowther 1961, Lowther and Falls 1968, Atkinson and Ralph 1980, pers. obs.) and in karyotype (Thorneycroft 1976), and morphometric differences between morphs have been correlated with karyotype (Rising and Shields 1980). This polymorphism appears to be maintained by negative assortative mating; white-striped (WS) birds of either sex usually pair with tan-striped (TS) birds of the opposite sex (Lowther 1961, Thorneycroft 1976, Knapton and Falls 1983). Furthermore, there are ecological differences between morphs: Knapton and Falls (1982) found that the range of habitat types occupied by WS and TS males was different; WS males defended territories in "open" habitat whereas TS males defended territories in a broader range of habitat, from "open" to "dense." Possible explanations for this difference in habitat occupancy are: (1) WS males dominate TS males in territorial encounters, establish territories in optimal habitat, and force some TS males into suboptimal habitat. (2) WS males arrive on the breeding grounds before TS males, occupy the "best" areas, and force TS males to take territories in suboptimal areas. In either case, some measure of reproductive fitness should be lower in TS males. (3) TS males achieve, over a broad range of habitat types, a reproductive fitness which is equivalent to that of WS males in a narrower range. In this paper, we investigate the arrival dates, breeding ecology, and reproductive success in populations of WS and TS birds to determine if differences occur between morphs.

Aspects of the breeding biology of the White-throated Sparrow have been studied by Lowther (1960, summary in Lowther and Falls 1968) and Wasserman (1980); however, these workers did not examine differences in the breeding ecology of the two morphs. Knapton and Falls (1983) showed differences between morphs in parental contribution to feeding nestlings. Here we compare morphs with the following questions: (1) Does time of arrival on the breeding grounds differ? (2) Are there different degrees of site tenacity? (3) Are there differences in breeding biology—in clutch-size, clutch initiation, growth of nestlings, and number of young fledged per nest?

METHODS

We carried out the study in Algonquin Provincial Park, Nipissing District, Ontario, during the spring and summer of 1979, 1980, and 1981. The following study areas were used: (1) around the periphery of the Lake of Two Rivers airfield (Airfield), (2) at Pog Lake, and (3) near the Pioneer Logging Exhibit (PLE). Distances between study areas ranged from 6 km (Airfield–Pog Lake) to 24 km (Airfield–PLE). We caught birds in mist nets, and banded each one with a unique color combination of plastic bands. Nestlings were banded at 5 days of age with unique plastic band combinations.

Nests were located by searching each study area. Most nests were discovered when the incubating bird was flushed; others were found by following adults carrying food. For each nest, we noted its location on aerial photographs (scale, 1 cm : 40 m), and the identity and morph of each parent. A log was kept for each nest until it was empty: either the young fledged or the nest contents were robbed. Thus, we could determine success rate, and length of incubation and nestling periods, for each of the two main pair types, WS male × TS female and TS male × WS female.

We determined the start of egg-laying from our own data and that of Lowther (1960). We assumed that one egg was laid per day and used day 0 as the start of incubation and day 12 as the day the eggs hatched. In the analysis of clutch intiation, we considered only those nests in which the first egg was laid in May in 1980, and in May and early June in 1981 (see below); thus, these were probably all first nesting attempts. In our comparison of clutch-size between morphs, we used only four and five egg clutches, and only those nests in which clutch-size remained constant for three or more days.

We determined growth rates of young White-throated Sparrows as follows. Each nestling was weighed to the nearest 0.5 g every day until it fledged or disappeared (presumably through predation) from the nest. Each nestling was marked on the tarsus with a felt marker, and therefore we could identify individuals within each nest from one day to the next. In the analyses, we compared growth of the nestlings between parental female morphs and between brood-sizes. Day by day comparisons of nestling weights were made with *t*-tests and two-way analysis of variance (by morph and clutch-size).

RESULTS

Arrival on breeding grounds.—White-throated Sparrows arrived on the study areas from the last few days of April to mid-May. Males arrived before females in 1980 and 1981 (observations in 1979 started in mid-May, after the males had arrived). Fig. 1 shows cumulative arrival frequencies for males and females of both morphs in 1980; the trends were similar in 1981.

The period of arrival was broad for both WS and TS males (Fig. 1). Cumulative territorial occupancy at 90% was reached in about 15 days by both morphs in 1980 (Fig. 1) and in about 14 days in 1981. Hence the length of the arrival period did not appear to differ between male morphs.

WS males seemed to arrive slightly earlier than TS males. In 1980, 58.7% (27/46) of WS males arrived by 6 May compared to 42.9% (9/21) of TS males, and in 1981, 64.3% (27/42) of WS males arrived by 5 May

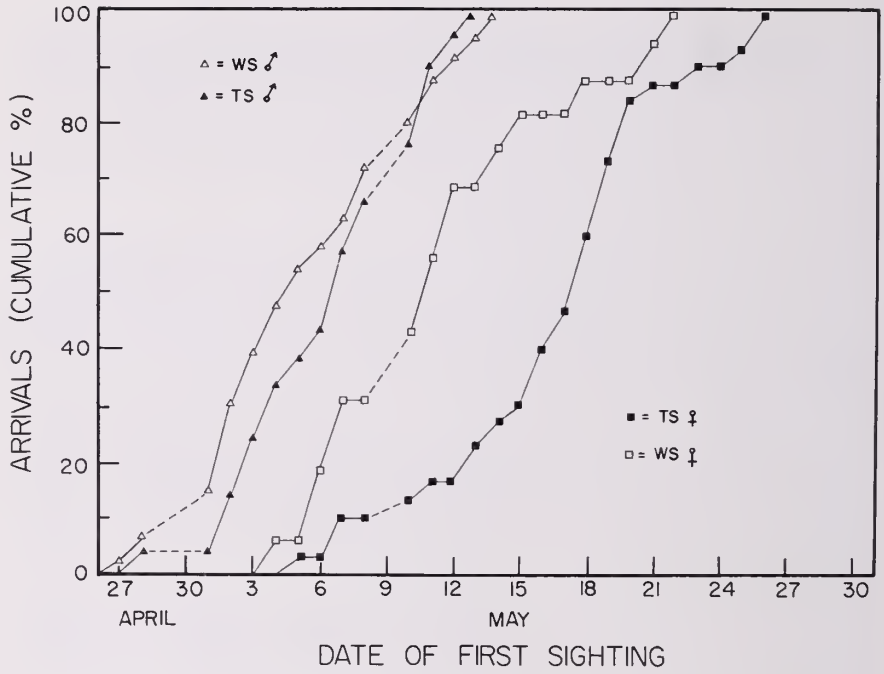

FIG. 1. Cumulative arrival frequencies of WS and TS male and female White-throated Sparrows, 1980 data. Data for 1981 follow similar trends. No mistnetting was done on 29 and 30 April, and 9 May. Numbers for each morph-sex class were 46 WS males, 21 TS males, 30 TS females, and 16 WS females.

compared to 52.2% (12/23) of TS males; however, neither difference is significant (1980: $\chi^2 = 0.88$, df = 1, NS; 1981, $\chi^2 = 0.47$, df = 1, NS).

WS females were detected significantly earlier than TS females in both years. Of 46 females (16 WS, 30 TS) identified in May 1980, 12 WS and only eight TS were detected by 14 May ($\chi^2 = 7.97$, df = 1, $P < 0.01$); of 24 females (10 WS, 14 TS) identified in May 1981, nine WS and three TS were detected by 14 May (Fisher's exact test, $P < 0.004$).

Site tenacity.—In total, we banded 340 adults: 176 in 1979, 103 in 1980, and 69 in 1981. We color banded 65 nestlings in 1980.

A comparison of return rates between males of the two morphs revealed no differences for all study areas combined (Table 1). Twenty-three of 46 WS males and 11 of 21 TS males returned in 1980 ($\chi^2 = 0.007$, df = 1, NS), and 20 of 42 WS males and 9 of 23 TS males returned in 1981 ($\chi^2 = 0.55$, df = 1, NS). The number of returning WS males varied from 50.0% (1979–80) to 47.6% (1980–81), and that of TS males from 52.4% (1979–

TABLE 1
RETURN RATES OF MALE WHITE-THROATED SPARROWS OF BOTH MORPHS TO THE STUDY AREAS

Study area	No. territorial males (1979)	No. returning males (1980)	WS	TS
PLE	31	19 (61.3%)	15/22 (68.2%)	4/9 (44.4%)
Airfield	22	11 (50.0%)	6/14 (43.0%)	5/8 (62.5%)
Pog Lake	14	4 (28.6%)	2/10 (20.0%)	2/4 (50.0%)
Total	67	34 (50.7%)	23/46 (50.0%)	11/21 (52.4%)
	(1980)	(1981)	WS	TS
PLE	30	14 (46.6%)	11/23 (47.8%)	3/7 (42.9%)
Airfield	22	9 (40.9%)	5/12 (41.7%)	4/10 (40.0%)
Pog Lake	13	6 (46.2%)	4/7 (57.1%)	2/6 (33.3%)
Total	65	29 (44.6%)	20/42 (47.6%)	9/23 (39.1%)

80) to 39.1% (1980–81). These return rates are probably conservative, as some males returned to the study areas but not to the same territories occupied the previous year. Thus, a male that returned to take a territory just outside the study areas would have gone undetected.

Return rates of females were very low. Only three females out of 55 banded in 1979 returned in 1980, a return rate of 5.5%. All three were WS, and two returned to the same territories occupied the year before, but to different mates. Four females (three WS, one TS) out of 43 banded in 1980 returned in 1981 (9.3%), two of these females returning to the same territory occupied in 1980. During 1981, we did not see any of the 65 nestlings color-banded in 1980.

The nesting season.—Forty-three nests were found in 1980 and 24 in 1981. Nests were found at various stages of the breeding cycle, and therefore not all nests could be used in each analysis.

Clutch initiation.—In 1980, we located 14 nests in which the first egg was laid in May, and therefore probably were all first nests. Seven nests were of TS male × WS female pairs, and seven of WS male × TS female pairs. The dates of first eggs laid are as follows: TS male × WS female—19, 22, 22, 23, 25, 26, 26 May; WS male × TS female—27, 27, 27, 28, 28, 28, 31 May. From this sample, a clear separation in clutch initiation between morphs appeared ($R = 2$, $P < 0.05$ Wald-Wolfowitz runs test). In 1981, the calculated laying date of the first egg was 28 May, 9 days later than in 1980. In 1981, 15 probable first nests were initiated between 28 May and 6 June, as follows: TS male × WS female—29, 31, 31 May,

TABLE 2
COMPARISON OF CLUTCH-SIZE BETWEEN FEMALE MORPHS DURING MAY, JUNE, AND JULY

	Clutch-size	May		June		July		Total	
		WS	TS	WS	TS	WS	TS	WS	TS
1980									
	4	2	6	4	9	1	2	7	17
	5	5	0	2	4	0	0	7	4
1981									
	4	0	1	8	7	0	0	8	8
	5	0	0	1	3	0	0	1	3

1, 5 June; WS male × TS female—28, 29, 29, 29, 29 May, 3, 3, 4, 5, 6 June. There was no difference between morphs in clutch initiation ($R = 7$. $P > 0.05$, Wald-Wolfowitz runs test).

Clutch initiation of WS male × TS female pairs was similar between years ($R = 6$, $P > 0.05$, Wald-Wolfowitz runs test). On the other hand, clutch initiation of TS male × WS female pairs was much later in 1981 ($R = 2$, $P < 0.05$, Wald-Wolfowitz runs test); there was about a 10-day difference between years.

Clutch-size.—We used a sample of 55 nests (35 in 1980, 20 in 1981) in this analysis. Forty of these were four-egg and 15 were five-egg clutches (Table 2).

Clutch-sizes did not differ between females of the two morphs in either year. In 1980, TS females had 17 four-egg and 4 five-egg clutches whereas WS females had 7 four-egg and 7 five-egg clutches ($P = 0.060$, Fisher's exact test). In 1981, TS females had 8 four-egg and 3 five-egg clutches, and WS females had 8 four-egg and 1 five-egg clutches ($P = 0.932$, Fisher's exact test).

Clutch-sizes did not differ between years for either morph. For WS females, there were 7 four-egg and 7 five-egg clutches in 1980, and 8 four-egg and 1 five-egg clutches in 1981 ($P = 0.069$, Fisher's exact test). For TS females, there were 17 four-egg and 4 five-egg clutches in 1980, and 8 four-egg and 3 five-egg clutches in 1981 ($P = 0.983$, Fisher's exact test). Thus, clutch-size was not affected by the later onset of nesting in 1981.

Success rates.—In this analysis, a successful nest is defined as one from which one or more young fledged. Success rates were 54% for TS females and 50% for WS females in 1980, and 46% for TS females and 45% for WS females in 1981 (Table 3). There were no differences between morphs

TABLE 3
COMPARISON OF SUCCESS RATES OF NESTS BETWEEN WS AND TS FEMALES

Study area (year)	Total no. nests	No. successful nests	Success rates	
			TS female	WS female
1980				
All study areas	38	20 (53%)	13/24 (54%)	7/14 (50%)
1981				
All study areas	24	11 (45%)	6/13 (45%)	5/11 (45%)
1980 + 1981				
PLE	26	18 (69%)	13/21 (62%)	5/5 (100%)
Other areas	36	13 (36%)	6/16 (38%)	7/20 (35%)

in success rates (1980—χ^2=0.06, df = 1, NS; 1981—χ^2 = 0.14, df = 1, NS).

However, there were differences among study areas. Success rate at the PLE was 69% (18 out of 26 nests), whereas that for all other study areas combined was only 36% (13 out of 36 nests) (Table 3, $\chi^2 = 6.63$, df = 1, $P < 0.05$). Observer activity at nests did not vary among study areas, and most nest contents were lost to predation, which accounted for 74% of egg losses and 75% of losses of young. This implies that predation was less intense at PLE than elsewhere. Linings of most robbed nests were disturbed, suggesting mammalian predation. Signs and sightings of two potential mammalian predators, marten (*Martes martes*) and red fox (*Vulpes fulva*), were more frequent at the Airfield than elsewhere, which may help to explain the lowered success rates there.

The number of nests found in 1980 was 38 (Table 3). Six pairs renested, one pair was double-brooded (see below), therefore we have success rates of 31 males. Twenty of these males were successful, and of these 20, eight (six WS, two TS) returned in 1980. Of the 11 unsuccessful males, six (four WS, two TS) returned. Thus, successful males are no more likely to return the next year than unsuccessful ones ($\chi^2 = 0.17$, df = 1, NS). Only one female (WS) of the 31 pairs returned in 1981; she had successfully raised young in 1980.

Nesting mortality.—There was no consistent difference in number of fledged young between WS and TS females during 1980 and 1981 (Table 4). TS females fledged proportionately more young than WS females in 1980 (50%:43%) but fewer young in 1981 (37%:49%). Differences were not significant in either year (1980—χ^2 = 0.48, df = 1, NS; 1981—χ^2 =

TABLE 4
COMPARISON OF HATCHING AND FLEDGING SUCCESS BETWEEN FEMALE MORPHS

	1980		1981		1980 + 1981	
	TS	WS	TS	WS	TS	WS
No. eggs laid	84	63	57	41	141	104
No. eggs hatched	63 (75%)	44 (70%)	36 (63%)	28 (68%)	99 (70%)	72 (69%)
No. young fledged	42 (50%)	27 (43%)	21 (37%)	20 (49%)	63 (44%)	47 (45%)

0.95, df = 1, NS) or for both years combined (1980 + 1981, $\chi^2 = 0.003$, df = 1, NS).

There was no relationship between age of young and risk of predation (Table 5). Eggs hatched in 23 nests, hence we could estimate the age of nestlings in these nests to within a day. Young fledged from 11 of these nests, and the rate of predation on the other 12 nests was relatively uniform. Thus, predation rates did not increase with age of young or increased parental activity at the nest.

Length of nestling period.—We used day 0 as the day on which the eggs hatched, and recorded the days when young were in the nest. Table 5 shows that young fledged at day 9 from 9 of the 11 nests that were followed from hatching to fledging. Young from the remaining two nests left at day 8 and day 10 respectively. Six of the female parents were TS, five were WS, and there were no differences between morphs in the length of nestling period.

Second broods.—The information on double-broodedness refers to the PLE study area. Eleven pairs fledged young before 7 July; of these 11, six (54.5%) attempted second broods (four WS × TS and two TS × WS pairs). A breakdown of these six is as follows: a second nest, later robbed, was found for one pair, three pairs were found with young barely able to fly in late July and August, and two pairs were seen carrying food and giving distraction displays (approach within 1 m of observer, high rate of alarm calls, "broken wing" display) in early August. Loncke and Falls (1973) related double-broodedness to high populations of spruce budworm (*Choristoneura fumiferana*). This was probably not a factor in 1980 as budworm populations were not particularly high (Howse et al. 1981). White-throated Sparrows are probably frequently double-brooded provided that they raise one brood early enough to allow them sufficient time to attempt a second brood. As in other studies of White-throated Sparrows (e.g., Lowther 1960), we found renesting to be common.

TABLE 5
AGE OF NESTLINGS AND RATE OF PREDATION

	Day										
	0	1	2	3	4	5	6	7	8	9	10
No. active nests	23	22	21	18	15	14	13	11	10	1	0
No. empty nests	0	1	1	3	3	1	1	2	0	0	0
No. successful nests[a]	—	—	—	—	—	—	—	—	1	9	1

[a] Nest empty; young out of the nest nearby.

Growth rates of nestlings.—We found no significant differences in nestling weight at any age (from hatching to fledging) between female morphs, and furthermore there were no significant differences in nestling weight between brood-sizes of three and four (t-tests, $P > 0.05$, Fig. 2 and Appendix). Finally, we found no significant differences in nestling weight when female morph and brood-size are considered together (two way analysis of variance, $P > 0.05$).

DISCUSSION

As mentioned earlier, Knapton and Falls (1982) found that WS males defended territories in a narrower range of habitat types than did TS males. To reiterate two possible explanations: (1) WS males dominate TS males in territorial encounters and thus come to occupy the optimal habitat, forcing some TS males into suboptimal habitat; and (2) WS males arrive on the breeding grounds before TS males, occupy the "best" areas, and in this way cause TS males to take territories in suboptimal areas. In either case, some measure of reproductive fitness should be lower in TS males than in WS males.

Our analyses support neither explanation. There was no obvious dichotomy of arrival between male morphs. Total arrival periods for males were equally broad for each morph, and birds of both morphs returning from the previous year appeared on the study areas throughout the arrival period, not necessarily at the beginning. Although WS males arrived slightly earlier, the differences between morphs were not significant. Furthermore, TS males are more cryptic in behavior than WS males (pers. obs.), and hence are more likely to be overlooked. WS females were detected earlier than TS females; however, not only are TS females more cryptic than WS females, but a female tends to be detected when she is already associating with a male, hence the actual arrival dates of all females may be earlier than indicated. Possibly, these results indicate that pair for-

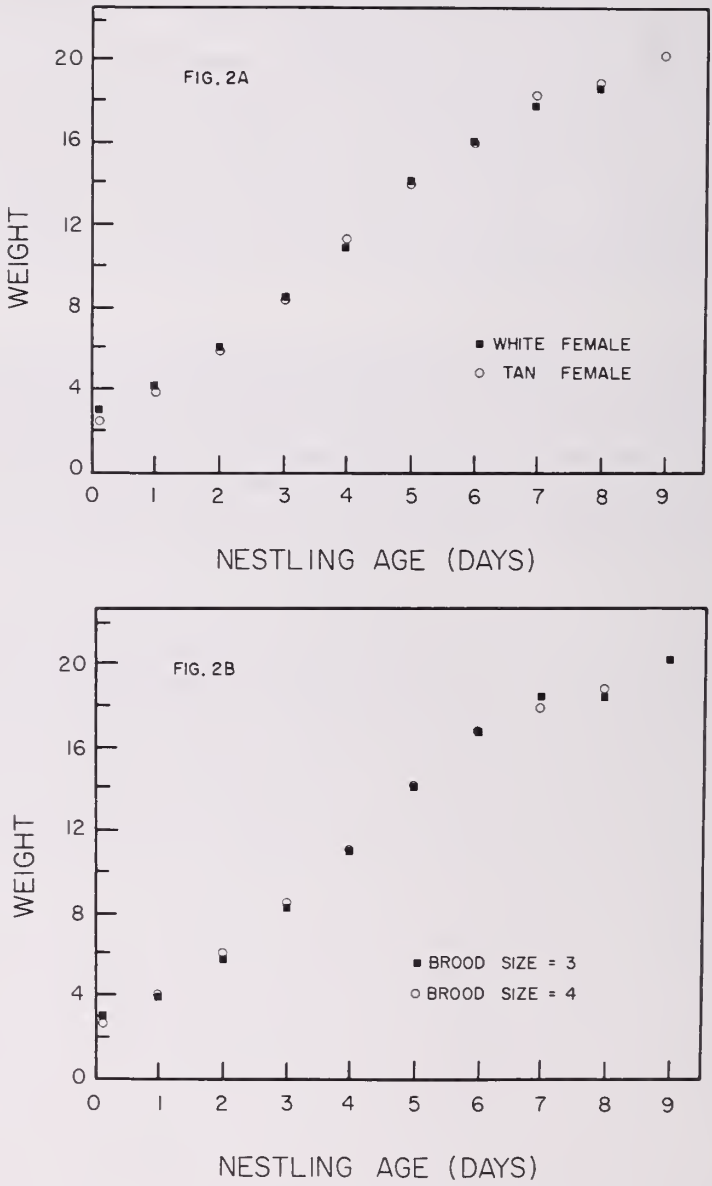

FIG. 2. Comparisons of nestling age with weight (g) between female morphs (2A) and between brood-size (2B).

mation is quicker in TS male × WS female pairs, rather than an earlier arrival of WS females.

If WS males dominated or arrived before TS males, then one might predict that WS males would show a higher rate of return than TS males in subsequent years. We detected no such difference in rate of return between males of the two morphs to the study areas.

Clutch intiation in 1980 was significantly earlier in TS × WS pairs than in WS male × TS female pairs, but was similar between pair types in 1981. The difference in 1980 could be explained either by an earlier arrival of WS females or by quicker pair formation in TS male × WS female pairs. Cumulative arrival data show a broad overlap in time of arrival of females of both morphs. Thus, we are left with the argument that pair formation is quicker in TS male × WS female pairs, and, under certain environmental conditions, this can result in an earlier onset of clutch initiation.

Success rates of nests, number of young fledged per nest, length of nestling period and growth rates of nestlings did not differ between morphs. Therefore the argument that TS males suffer reduced reproductive fitness because they are in suboptimal habitat does not seem convincing. We cannot compare contributions to future gene pools between morphs as no banded nestlings returned to breed on the study areas in subsequent years. Young of WS and TS females fledged at similar weights, however, and if weight at fledging reflects future survival, then there is no indication that the young of one morph differed from those of the other. Thus, the argument that TS males suffer a reproductive cost by occupying "suboptimal" habitat is not supported.

TS males sing less (Lowther and Falls 1968), are less responsive to song playback than WS males on the breeding grounds (J. Jones, pers. comm.), and initiate fewer aggressive encounters (Ficken et al. 1978), while their level of contribution to feeding young is significantly greater (Knapton and Falls 1983), than that of WS males. These behavioral differences suggest that if TS males are indeed forced into suboptimal habitats, they maximize their fitness by apportioning more time and energy into parental care and less into territory defense and advertisement.

SUMMARY

We compared breeding ecology and reproductive success between morphs of the White-throated Sparrow (*Zonotrichia albicollis*). Total arrival time was equally broad for both white-striped (WS) and tan-striped (TS) males, and no difference was found in time of arrival on the breeding grounds between male morphs. WS females were detected significantly earlier than TS females; this is possibly a result of quicker pair formation in TS male × WS female pairs as clutch initiation was earlier in this pair type in one year than in WS male ×

TS female pairs. Return rates of males to the study areas in successive years did not differ between morphs; return rates of females were very low in all years.

Success rates of nests, number of young fledged per nest, length of nestling period, growth rates of nestlings, and weight of nestlings at fledging did not differ between morphs. Thus, the argument that TS males suffer a reproductive cost by occupying "suboptimal" habitat is not supported.

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Appendix

Growth Rates (Wgt. in g) of Nestling White-throated Sparrows with Respect to Morph of Female and Brood-size

	TS female			WS female		
Age	N	$\bar{x}$	±SD	N	$\bar{x}$	±SD
0	23	2.6	0.5	26	3.0	0.9
1	32	3.8	0.7	34	4.2	1.2
2	32	6.0	1.3	30	6.0	1.5
3	28	8.4	1.4	27	8.6	1.7
4	25	11.2	1.6	22	10.8	2.0
5	22	14.0	1.5	22	14.1	1.9
6	15	16.0	1.6	22	15.9	1.7
7	16	18.3	1.8	19	17.7	1.7
8	9	18.8	1.2	10	18.5	1.7
9	2	20.3	0.2			
	Brood-size 3			Brood-size 4		
Age	N	$\bar{x}$	±SD	N	$\bar{x}$	±SD
0	15	2.9	0.7	28	2.6	0.6
1	21	3.8	0.9	40	4.0	1.0
2	21	5.7	1.6	36	6.1	1.3
3	18	8.3	1.6	32	8.6	1.5
4	15	11.0	2.1	32	11.0	1.7
5	12	14.1	1.6	32	14.0	1.7
6	9	16.6	1.2	28	15.7	1.7
7	3	18.4	1.6	32	17.9	1.8
8	1	18.4	—	18	18.7	1.4

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TERRITORY PREFERENCE OF VESPER SPARROWS IN CROPLAND

Louis B. Best and Nicholas L. Rodenhouse

The Vesper Sparrow (*Pooecetes gramineus*) is an abundant species breeding in much of the cultivated land that extends across the plains and prairies of North America (Stewart and Kantrud 1972, Mikol et al. 1979, Dinsmore 1981, Henderson 1981). In central Iowa, Vesper Sparrows commonly establish territories along fencerows between fields of corn and soybeans. This sparrow sings primarily from fencerows and forages along their edges, but places its nest on the ground in the crop field. Despite the species' abundance in cropland, in some areas its productivity in this habitat may be below that needed to offset adult mortality (Rodenhouse and Best 1983). The question might then be asked, is the Vesper Sparrow preadapted to make an inappropriate choice in selecting agricultural cropland for breeding?

Vesper Sparrows are found in a variety of habitats other than corn and soybean fields (Rodenhouse 1981) but are associated with similar habitat characteristics in each. Typically, the species breeds in sparsely vegetated areas (Sutton 1960, Berger 1968, Wiens 1969, Whitmore 1979) and xeric sites (Grinnell and Miller 1944). Breeding Vesper Sparrows occur in very low densities, if at all, in areas with dense vegetation (Dambach 1948, Graber and Graber 1963). Preceding human settlement, the open xeric or disturbed sites used by Vesper Sparrows were maintained by fire (e.g., jack-pine [*Pinus banksiana*] stands in Michigan [L. H. Walkinshaw, unpubl.]), erosion of loose soils by wind (e.g., sand dunes [Olson 1958]), or overgrazing by bison (*Bison bison*) (Owens and Myers 1973). In the Midwest, Vesper Sparrows now breed primarily in areas disturbed annually by cultivation.

The objectives of this study were to (1) identify habitat characteristics preferred by Vesper Sparrows that establish territories in cropland; (2) determine the relationship between territory preference and nesting success; and (3) evaluate the adaptiveness of breeding on agricultural land.

METHODS

Study sites.—The study was conducted in Story County, Iowa, in 1979 and 1980. Study sites were selected in upland areas that contained a fencerow at least 300 m long between a corn and a soybean field. Eight sites were used in 1979; 13 additional sites were added in 1980. Study sites included the portion of the crop field on both sides of the fencerow that was used by Vesper Sparrows. Vegetative cover of fencerow study sites ranged from those dominated by grasses with negligible shrub (woody growth 1–3 m tall) cover, to fencerows

with high shrub coverage and low grass coverage. Trees (>3 m tall) occurred rarely on fencerows. Fencerows with greater shrub coverage were wider (Spearman's rank correlation, $r_s = 0.53$, $N = 31$, $P < 0.01$) and had higher plant species richness ($r_s = 0.73$, $P < 0.01$). Corn and soybeans were rotated annually on all fields studied.

Field methods.—Vegetation was measured every 20 m along fencerows on a representative sample (14) of the study sites. Sample plots were 0.5 m wide, with a variable length that corresponded to the fencerow width (distance between tilled fields). Canopy coverage of all plant species and growth forms (grasses, forbs, shrubs, and trees) within sample plots was estimated visually.

The location and height of all shrub groups along each fencerow were recorded. Shrub groups included one or more shrubs or saplings that formed a contiguous canopy. On fencerows planted with multiflora rose (*Rosa multiflora*), saplings or shrubs extending above the continuous rose hedge were designated shrub groups. The amount of crop residue was measured before planting by using the "bead-string" method (Sloneker and Moldenhauer 1977). At least three sites were sampled in each field at 80-m intervals along the fencerow. Each sample began 15 m from the fencerow and extended outward into the field, at a 45° angle to the crop rows.

Territories were located by walking along fencerows and observing singing males. Males singing from mid-field (usually about 200 m from a fencerow) as well as along fencerows could be detected easily. Attempts to delimit territories by using the repeated flushing technique (Wiens 1969) were only partly successful; territories were well-defined near fencerows but not in the crop fields. As many males and females as possible (26 and 11, respectively) were mist-netted and marked with colored leg bands and a U.S. Fish and Wildlife Service band in 1980. We visited each study site in the spring of 1981 to determine if any banded birds had returned, but did not search neighboring areas.

Agriculturally nonproductive areas on and surrounding each territory were mapped, and their coverages were estimated. "Nonproductive areas," other than fencerows, included grassy waterways (uncultivated watercourses covered by a grass sod), washes (cultivated watercourses where erosion severely stunted crop and weed growth), and weedy areas (low wet areas where crop growth was stunted by flooding or rank weed growth).

Territories on which nests were not found during routine visits were systematically searched for nests. Territories usually were visited every 4 days, and active nests were checked at least every other day.

Analysis methods.—The following territory characteristics were used as variables in evaluating territory preference and nesting success: number of shrub groups (within the fencerow), fencerow coverage, number of washes, crop residue before planting, and coverage of nonproductive areas (other than fencerows). These variables were selected because they represent the major structural and vegetational features within Vesper Sparrow territories. Because our data did not meet the assumptions of normality and homogeneity of variance required for parametric statistics, we tested for statistical significance by using a nonparametric procedure (Kruskal-Wallis one-way ANOVA, Nie et al. 1975). Statistical significance was set at $P \leq 0.05$.

RESULTS AND DISCUSSION

General breeding ecology.—Male Vesper Sparrows arrived unpaired and established territories during the first 3 weeks of April; most arrived before spring field operations for crop production had begun. Females began arriving within a week of the first males. Territories were situated along fencerows and usually extended no more than 80 m into the crop

field on both sides of the fencerow. (Rodenhouse and Best [1983] describe territory characteristics in detail.) Breeding densities were greater along fencerows with more shrubs.

Early in the breeding season, males sang primarily from the fencerows (using shrubs, fenceposts, and fence wire for song perches), whereas late in the season, they sang most frequently from perches in crop fields. Early nests were built in a clump of crop residue and were concentrated in fields with the most crop residue (i.e., corn residue). Once spring tillage began and initial nests were destroyed, nest placement shifted from one side of the fencerow to the other, away from the side most recently tilled. After the crop was approximately 10 cm tall, nests were placed at the base of the growing plants. Late in the season when the crop canopy closed, washes in soybean fields were used heavily as nest-sites. Nesting success on cropland was low (13% overall [Rodenhouse and Best 1983]), particularly early in the breeding season. Nest losses resulted primarily from agricultural field operations and predation.

Territory preference.—To identify territory characteristics preferred by Vesper Sparrows, we looked for significant relationships between variables measured on each territory and two indirect measures of territory preference: arrival date of males and pairing success. Territories occupied first were considered most preferred, and territories of paired males were considered more preferred than those of unpaired males. Males that arrived late were more likely to remain unmated. Sixteen of 17 males that arrived during the first week and 19 of 20 in the second week acquired mates, whereas only three of five males that arrived during the third week paired successfully.

Males arrived earlier on areas where fencerows had a greater number of shrub groups (Table 1). Although not statistically significant ($P = 0.1$), crop residue on fields tended to be greater and the areal coverage of fencerows less on territories occupied early. Pairing success was related significantly to the number of shrub groups and the amount of crop residue within territories and almost significantly ($P = 0.06$) to the coverage of nonproductive areas (other than fencerows) (Table 1).

Elevated perches, potentially used for singing, are associated with Vesper Sparrow territories in many uncultivated habitats: shrubs and fenceposts in pastured areas (Wiens 1969) and western rangelands (Mikol et al. 1979); woodlands bordering old fields (Sutton 1960, Berger 1968) or reclaimed surface mines (Wray et al. 1982); and shrubs in sagebrush-grassland (Feist 1968, McGee 1976, Mikol et al. 1979), pinyon-juniper (O'Meara et al. 1981), or young jack-pine communities (L. H. Walkinshaw, unpubl.). Although the species nests in open, sparsely vegetated areas, elevated song perches seemingly are a territory requisite. We found

TABLE 1

RELATIONSHIPS BETWEEN HABITAT CHARACTERISTICS OF VESPER SPARROW TERRITORIES ($\bar{x}$ AND RANGE) AND EITHER DATE OF ARRIVAL OF MALES OR PAIRING STATUS

Habitat characteristics	Date of arrival[a]					Pairing status			
	Week 1 (17)[b]	Week 2 (20)	Week 3 (5)	χ^2[c]	*P*	Paired (38)	Not paired (4)	χ^2	*P*
Shrub groups (N)	5.2 (0–16)	3.1 (0–11)	1.2 (0–6)	8. 17	0.02	4.1 (0– 16)	0 (0)	8.16	<0.01
Washes (N)	0.6 (0–2)	0.8 (0–2)	0.6 (0–2)	0.46	0.79	0.7 (0–2)	0.3 (0–1)	1.32	0.25
Crop residue[d] (kg/ha)	2730 (560–5040)	2440 (560–6050)	1320 (560–2470)	4.57	0.10	2570 (560–6050)	1040 (560–2470)	4.53	0.03
Fencerow coverage (m^2)	330 (120–610)	410 (230–790)	410 (350–520)	4.39	0.11	380 (120–790)	360 (200–520)	<0.01	0.95
Nonproductive areas[e] (m^2)	970 (0–3000)	1510 (0–5820)	1730 (0–4260)	1.48	0.48	1410 (0–5820)	400 (0–1030)	3.48	0.06

[a] The week during which the first males arrived was designated Week 1.
[b] Number of territories established during each week of arrival.
[c] χ^2 determined using Kruskal-Wallis one-way ANOVA.
[d] Amount on field with the most crop residue; on 40 of 42 territories the crop residue was corn.
[e] Includes grassy waterways, washes, and weedy areas.

that elevated perches (i.e., fencerow shrubs) enhanced territory preference (Table 1) and evidently affected territory location; 50 of the 51 territories located were associated with a fencerow.

Territory selection by Vesper Sparrows on corn and soybean fields may be related to the abundance and availability of foods fed to nestlings. Adults feed on both plant and animal materials (Evans 1964), and weed seeds (likely an abundant food resource along fencerows) constitute a large portion of their diet throughout the breeding season in both cultivated (Rodenhouse and Best, unpubl.) and uncultivated (Evans 1964) habitats. Nestlings, however, are fed almost exclusively animal foods, primarily insects (Evans 1964; Rodenhouse and Best, unpubl.), and insects are scarce in crop fields early in the breeding season (Price 1976).

Insects associated with cropland are most abundant in nonproductive areas (e.g., fencerows) (Dambach 1948, Wunz 1952) that serve as sources from which many insects colonize crop fields (Price 1976). Additionally, insects are more numerous on fields with more crop residue (Dambach 1948, Edwards and Lofty 1969). Vesper Sparrows concentrated their foraging activity near nonproductive areas, particularly early in the breeding season (85% of all foraging observations recorded before 31 May were ≤ 10 m from a nonproductive area; Rodenhouse and Best, unpubl.). Therefore, to maximize abundance of insect foods on their territories, one would expect Vesper Sparrows to select areas with the most crop residue and the greatest number or coverage of nonproductive areas. We found significant or nearly significant, positive relationships between the two measures of territory preference and the amount of crop residue, coverage of nonproductive areas, and coverage of fencerows (Table 1). That preferred territories contained fencerows with a greater number of shrub groups (and plant species richness; see Methods) also may represent a response by Vesper Sparrows to food availability. Fencerows with high structural diversity and species richness support more abundant and diverse insect communities (Dambach 1948, Wunz 1952). Because various insect species reach peak densities at different times (Dambach 1948, Pimentel 1961, Mayse and Price 1978, Maher 1979), nestling foods may be most consistently available where insect communities are diverse.

The significant relationship between quantity of crop residue on a territory and pairing success also suggests that Vesper Sparrows may assess availability of nest-sites during territory selection. Early in the season, nests were always placed in a clump of crop residue, and the amount of crop residue may affect concealment of the nest and (or) of birds as they approach the nest.

Although we did not evaluate directly the relative advantages of selecting a territory containing only one crop type vs two (see Methods),

two observations suggest that Vesper Sparrows may have benefitted from including both corn and soybean fields within their territories. First, field operations on opposite sides of the fencerow were asynchronous, and each field was tilled approximately every 2 weeks through late June (Rodenhouse and Best 1983). Although nesting sparrows were disturbed regularly and nests often were destroyed, only part of the territory was tilled at one time, leaving the birds a refuge within their territories. Nesting success probably was not increased by including both corn and soybean fields, but the likelihood of territory desertion may have been decreased. Secondly, weedy areas under the corn canopy received heavy use as foraging sites in late June and early July (overall, adults foraged for food for their young most frequently in soybean fields [61% of a total of 1991 foraging observations], but during 27 June–10 July, corn fields were used more heavily [56% of 403 foraging observations]; Rodenhouse and Best, unpubl.). Corn fields were too densely vegetated by late June to be suitable for nesting, but soybean fields were not. Consequently, adjacent corn and soybean fields provided suitable nesting sites and preferred foraging sites in close proximity during a period of the breeding season when the probability of successful nesting was highest.

Site fidelity.—Of 26 male and 11 female Vesper Sparrows banded in 1980, six (four males and two females) returned in 1981, all to the same fencerows they had used in 1980; two males occupied the same territories. All returning birds nested successfully (fledged at least one young) in 1980. Our data, and that of others (George [1952] and F. C. Evans [unpubl.] reported a return rate of about 50%), demonstrate site fidelity in this species.

Before pioneer settlement in the Midwest, the open xeric or disturbed sites used by breeding Vesper Sparrows usually occurred as patches within expanses of a given habitat. Such patches were maintained by fire, erosion of loose soils by wind, or overgrazing by bison. Although a particular site may have been suitable Vesper Sparrow breeding habitat for only a few years because of vegetation development, advantages gained from site fidelity evidently were great enough to favor its evolution. Site fidelity may have aided breeding birds in finding and defending a territory, and returning to a familiar site may have enabled birds to better exploit nesting and food resources (Best 1977).

The advantages of returning to a site on corn and soybean fields, however, are not readily apparent. Breeding habitat is abundant, and radical changes frequently occur on territories between breeding seasons—fencerows or fencerow shrubs may be removed and residue amounts may vary greatly depending on the crop grown, tillage practices, and weather. Thus, the location of suitable foraging and nesting sites and song perches may

TABLE 2

HABITAT CHARACTERISTICS ($\bar{x}$ AND RANGE) POTENTIALLY RELATED TO NESTING SUCCESS ON VESPER SPARROW TERRITORIES

Habitat characteristics	Number of successful nests			χ^2[b]	*P*
	0 (8)[a]	1 (16)	2 (11)		
Shrub groups (N)	6.3 (1–16)	3.6 (0–11)	3.3 (0–10)	4.29	0.11
Washes (N)	0.3 (0–1)	0.7 (0–2)	1.1 (0–2)	5.19	0.08
Crop residue[c] (kg/ha)	1760 (560–2910)	3070 (560–6050)	2390 (560–4480)	5.70	0.06
Fencerow coverage (m^2)	420 (310–730)	360 (120–620)	380 (190–790)	1.45	0.48
Nonproductive areas[d] (m^2)	1420 (0–3040)	1310 (0–5820)	1650 (100–4260)	0.99	0.61

[a] Number of territories sampled.
[b] χ^2 determined using Kruskal-Wallis one-way ANOVA.
[c] Amount on field with the most crop residue; on 33 of 35 territories the crop residue was corn.
[d] Includes grassy waterways, washes, and weedy areas.

be unpredictable from one year to the next; i.e., the old territory may be "unfamiliar." In fact, site fidelity on corn and soybean fields may result in some returning birds occupying suboptimal territories in preference to more favorable areas. These factors may, in part, explain our low rate of return in comparison to those of F. C. Evans (unpubl.) and George (1952).

Territory characteristics related to nesting success.—No territory characteristics were significantly related to nesting success, although the number of washes and amount of crop residue were nearly so ($P = 0.08$ and 0.06, respectively; Table 2). A nest was considered successful if it fledged at least one young.

Six of eight (75%) territories without a successful nest did not contain a wash, and territories with two successful nests (N = 11) had a mean of 1.1 washes. During the last month of the breeding season, washes in soybean fields were open areas in otherwise densely vegetated crop fields and were used heavily as nesting sites. As expected, the number of successful nests was closely related to the duration of territory occupancy ($r_s = 0.48$, N = 35, $P < 0.01$). Territories with at least one successful nest were occupied longer (by about 2 weeks) than those without a successful nest.

Because most Vesper Sparrow production occurred late in the breeding season, it would have been adaptive for Vesper Sparrows to select territories with washes in soybean fields (sites suitable for nesting during that

period), but we found no relationship between territory preference and the number of washes on a territory (Table 1). The potential location of washes is predictable from field topography at the time of territory selection, but the actual formation of washes may not be. Wash formation depends on crop type, weather, and residue amount. Where corn and soybeans are rotated annually, topographical conditions favoring wash formation within the territory must be present on both sides of the fencerow for a wash to be formed in a soybean field each year (assuming soybeans on one side of the fencerow and corn on the other). The development of washes depends on heavy rains and erosion during the period when soybean plants are small. Without such rains, potential wash sites may become as densely vegetated as the rest of the crop field. Because tillage practices differ among farm operators, the amount of crop residue within a territory may differ from one year to the next. Large amounts of crop residue slow water movement off the field, reducing the likelihood of washes being formed, whereas a lesser amount of crop residue may not prevent wash formation.

Although the amount of crop residue was related significantly to nesting success, we were unable to further define this relationship. Other factors that potentially influence nesting success (i.e., nest concealment, predation, parasitism) were not correlated with the amount of crop residue.

Adaptiveness of breeding on cultivated areas.—Territory selection is adaptive if preferred habitat characteristics are highly correlated with fitness, as measured by productivity (Hilden 1965, Verner 1975, Partridge 1978). Our results show relatively little correspondence between habitat characteristics associated with territory preference and those related to breeding productivity. We attribute this primarily to the disruptive effects of agriculture. Only the amount of crop residue was related positively to both territory selection and nesting success.

In uncultivated habitats, factors affecting nesting success and territory preferences of Vesper Sparrows are largely predictable. Nest failure is caused primarily by predators (Sutton 1960; Berger 1968; Wray et al. 1982; L. H. Walkinshaw, unpubl.), and nest predator densities probably are greatest at ecotones (Gates and Gysel 1978). Nest-site vegetational characteristics also influence nest vulnerability to predators (Wray and Whitmore 1979). Habitat changes do occur, but a given site probably provides breeding requisites for several years before vegetation development or some other factor makes it unsuitable. Over time, Vesper Sparrows have evolved behavioral responses to nest predation and predictable habitat changes.

Agriculture introduces nest losses that are not selective (i.e., either all nests are destroyed [e.g., during seedbed preparation], or nests are de-

stroyed in an unpredictable pattern) and radical "instantaneous" habitat changes (e.g., 100% of the crop residue may be buried in a day). In addition, later in the season after field operations are concluded, rapid and uniform crop development in the corn and soybean monocultures over broad areas effectively shortens the breeding season for many Vesper Sparrow pairs (few nesting sites are available). Because nest destruction by tillage operations is nonselective, there is little probability that Vesper Sparrows could adapt to this cause of mortality. Some agricultural habitat manipulations are largely predictable, but current farming methods have been used for only about 35 years and are still changing (Phillips et al. 1980). Thus, although Vesper Sparrows were pre-adapted to use disturbed land created by intensive agriculture, they may not be able to adjust to transitory farming methods.

SUMMARY

Vesper Sparrows (*Pooecetes gramineus*) commonly establish territories along fencerows in Iowa corn and soybean fields, where Vesper Sparrow productivity can be below replacement levels. We evaluated the adaptiveness of selecting territories on cultivated land by: (1) identifying habitat characteristics preferred by Vesper Sparrows (as measured by male arrival date and pairing success); and (2) determining the relationship between territory preference and nesting success. Males arrived earlier and had higher pairing success on territories where fencerows contained more shrub groups and where more crop residue was retained on the fields. The relationship of number of shrub groups and crop residue to various territory requisites (song perches, nestling food, and nest-sites) is discussed, as well as the implications of site fidelity in annually cultivated cropland. Nesting success was related to the number of washes and amount of crop residue on territories; both are unpredictable from year to year. Due primarily to the disruptive effects of agriculture, preferred habitat characteristics corresponded little with those related to productivity.

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CENSUSING BREEDING RED-WINGED BLACKBIRDS IN NORTH DAKOTA

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The amount of damage done to ripening agricultural crops in late summer in many regions of the United States appears to be closely related to population levels of breeding Red-winged Blackbirds (*Agelaius phoeniceus*) (Besser 1978, Dolbeer 1978, Meanley 1971). To aid in predicting damage by red-wings to ripening corn and sunflower crops in the Dakotas, biologists of the U.S. Fish and Wildlife Service have censused breeding male red-wings in roadside and non-roadside habitats in sample areas in a 77,700 km^2 area of North and South Dakota in 9 years since 1965 (Besser et al., unpubl.).

The area censused lies almost wholly within the Drift Plains physiographic region of the Northern Great Plains. It contains much of the wetland habitat remaining in the United States (Shaw and Fredine 1971) and some of the highest numbers of breeding Red-winged Blackbirds recorded on the North American Breeding Bird Surveys (Dolbeer and Stehn 1979). These populations contribute heavily to severe blackbird damage of ripening corn in South Dakota (De Grazio et al. 1971) and ripening sunflower in North Dakota (Henne et al. 1979); hence the interest in the population status of red-wings in this region.

In censusing red-wings, non-roadside habitats were sampled by walking 137-m-strip transects, in which a very high proportion of the breeding males were counted (Besser et al., unpubl.). Roadside habitats have been sampled by driving 137-m-strip transects at speeds ranging from 24–72 km/h, and consequently many breeding males are missed. The Hewitt (1967) sight-capture/sight-recapture method has been most commonly used to sample breeding red-wing populations in roadside habitats, but it involves making two trips over the same route, a major time constraint in censusing multi-county regions. The procedure used by USFWS biologists (Besser et al., unpubl.) involved only a single census of roadside habitats with an adjustment for males missed. This adjustment was initially based on calculations made from weekly censuses from May–July during two morning and two afternoon periods (De Grazio, pers. comm.). In 1980, to assess numbers of breeding male red-wings missed while censusing roadside populations and to determine why these males are missed, marked males were censused four times daily for a 10-day period which included most of the dates on which the 77,700 km^2 area was censused, and less regularly for a 63-day period thereafter.

METHODS

From 23–25 May 1980, 57 male Red-winged Blackbirds were captured on breeding territories along a 30.6 km route near Enderlin and Alice, Cass Co., in east-central North Dakota. Males were captured with traps described by Bray et al. (1975) and one leg was marked with a black-enamel, numbered 25 × 75 mm yellow-green streamer attached by an oversized USFWS band (as recommended by Guarino 1968). Twenty-seven of the tagged birds were also fitted with 1.7 g/164 mHz prototype leg transmitters described by Bruggers et al. (1981). These were attached to the other leg by two padded soft aluminum bands (split #7 size) placed 5 mm apart.

From 23–27 May the marked birds were monitored one or more times daily. During this period, we found that 5 of the 57 marked birds had much of their territorial areas more than 68.6 m from roads, the width of the strip transect recommended by Hewitt (1967); thus, observations of their activities were discontinued. An additional eight marked birds abandoned territories shortly after being marked. From 28 May–6 June the remaining 44 marked birds were monitored daily by one person during four periods: sunrise–10:00, 10:00–13:00, 15:00–18:00, and 18:00–sunset (DST). A second observer accompanied the driver on four occasions. The route was driven at a speed of about 48 km/h, but varied from 24–72 km/h depending on the visibility of each breeding territory and road conditions. The route was followed until the territory of a marked bird was reached and the bird not sighted. The driver then stopped and attempted to locate the marked bird.

To search for a non-radioed bird, the driver walked the road alongside its territory. To locate a radioed bird, the driver used a vehicle-mounted double-yagi antenna and a hand-held single-yagi in conjunction with LA-12 telemetry receivers (AVM Instruments). When a marked bird was found, it was tallied as present and its activity recorded. If the bird was not sighted or no signal was obtained within 3 min, it was tallied as absent and the driver resumed following the regular route. Marked birds were deemed to have abandoned and were dropped from the study the date after they were last encountered on a census. On 26 June, four of the tagged birds were shot by another person who notified the Bird Banding Office; these birds were excluded from the abandonment date analysis.

From 9 June–25 July, the route was run irregularly on 31 additional days during one or more of the four time periods. From 6 June–25 July, the status of nests on territories of 10 randomly chosen unmarked birds on roads adjacent to the study area were checked weekly to allow correlation of the nesting stages of females with the activity of territorial males. Temperature was recorded with a Weksler thermometer (Weksler Co., Freeport, New York) and wind speed with a Dwyer Wind Meter (Dwyer Instruments, Inc., Michigan City, Indiana) in open, unshaded areas at the beginning and end of the route each time the census was conducted.

RESULTS AND DISCUSSION

Date and time-of-day effects.—During the 10-day period (28 May–6 June) when most red-wing censuses have been conducted in the Dakotas, 76.1% (±SE 1.1%) of the marked males were seen on driven roadside transects (Table 1). Higher percentages of breeding red-wing males were observed during after-sunrise and before-sunset censusing periods from 28 May–26 June than during mid-day (see Tables 1 and 2), a pattern also recorded by Hewitt (1967) in New York.

From 28 May–6 June, 11 (27.5%) of 40 males abandoned, shifted

TABLE 1

PERCENT OF MARKED RED-WING MALES OBSERVED ON ROADSIDE TERRITORIES, 28 MAY–6 JUNE 1980

Date	N[a]	% (±SE) by time period (DST)				
		Sunrise–10:00 N[b] = 377	10:00–13:00 N = 378	15:00–18:00 N = 379	18:00–sunset N = 379	$\bar{x}$
28 May	44	84.1	68.2	75.0	81.8	77.3
29	44	85.7	55.8	75.0	77.3	73.5
30	44	79.5	70.5	59.1	75.0	71.0
31	42	66.7	73.8	81.0	81.0	75.6
1 June	38	78.9	60.5	68.4	76.3	71.0
2	35	74.3	74.3	77.2	91.4	79.3
3	34	85.3	73.5	73.5	85.3	79.4
4	33	69.7	78.8	69.7	78.8	74.2
5	33	84.8	81.8	75.8	72.7	78.8
6	32	84.4	78.1	71.9	87.5	80.5
$\bar{x}$		79.3 (±2.2)	71.5 (±2.6)	72.7 (±1.9)	80.7 (±1.9)	76.1 (±1.1)
Omitting 15:00–18:00						77.2 (±1.5)
Omitting 10:00–13:00 and 15:00–18:00						80.0 (±1.4)

[a] Number of males monitored.
[b] Number of observations.

territories, or were displaced from roadside territories, whereas from 7–16 June only 4 (13.8%) of the 29 remaining males gave up roadside territories (Fig. 1). As the first fledglings were not seen on territories of unmarked males in Cass County until after 6 June (Table 3), and many males feed older nestlings and fledglings in North Dakota (Besser, Brady, Burst, Minkoff, and Cummings, unpubl.) and elsewhere (Patterson 1979), it is unlikely that any of the males abandoning before 6 June produced young. From 17–26 June, the number of males abandoning territories increased to 32.0% (8 of 25). From 5–22 June, dates spanning the peak of incubation in 1980, fewer than 10% of the males abandoned roadside territories in any 3-day period (Fig. 1). Since the nesting season in 1980 was somewhat late (because of a 10-month drought that was not broken until 4 June), the period 1–10 June would probably be optimal most years for censusing red-wings involved in production of young in North Dakota.

Temperature and wind effects.—The data indicate that censuses should not be conducted when the temperature is above 27°C, particularly in mid-afternoon. In eight mid-afternoon censuses when temperatures were 27–34°C, we observed only 50.7% of the males on territory, whereas in 12 mid-afternoon censuses when temperatures were 9–26°C we observed

TABLE 2
PERCENT OF RED-WING MALES OBSERVED ON ROADSIDE TERRITORIES DURING FOUR TIME PERIODS, 9–26 JUNE 1980

Time period	Censuses	$\bar{x}$ (±SE) %
Sunrise–10:00	6	72.9 (±2.8)
10:00–13:00	5	62.6 (±2.8)
15:00–18:00	4	62.2 (±5.3)
18:00–sunset	6	66.8 (±2.2)
$\bar{x}$		66.5 (±1.6)
Omitting 15:00–18:00		67.4 (±3.0)
Omitting 10:00–13:00 and 15:00–18:00		69.9 (±3.0)

68.6% of the males, or 17.9% more ($P < 0.01$, $t = 2.95$, df = 17). Morning temperatures did not reach 27°C during any census in this study. Winds ranging up to 56 km/h had no effect on the percentage of males observed on territory. From 25 May–24 July, we observed 71.0% (± SE 2.1%) of the marked males on territory during 24 censuses, when winds were 26–56 km/h, whereas we saw 71.0% (±SE 1.5%) during 63 censuses when winds were 0–25 km/h.

Activities of missed roadside males.—Red-wings were not seen in 366 instances while censusing roadsides between 28 May and 6 June. These birds were off territories 65.8% of the time and were on territories, but hidden, 34.2% of the time. Of the 125 instances when birds were missed, but were on their territories, 102 were loafing, 12 were feeding, 9 were courting or chasing, and 2 were actually in view but seen by a second observer rather than the driver. Birds off territory were located in only 37 of 241 instances; of those birds located, 15 were feeding, 10 were chasing, 5 were loafing, and 7 were occupying a non-roadside territory.

Transmitter use and behavior of males.—In attaching the leg transmitters, we sometimes fractured the glass-like cyanoacrylate potting material by which transmitters were attached, resulting in their loss after only a few days of recorded activity. Thus, transmitters provided information for an average of only 6.7 days, range 1–25 days. The greatest distance moved recorded for a marked male was 2 km, and this bird had abandoned its original territory and moved to another. All feeding and chasing activities noted occurred within 1 km of the territory. Numbered leg streamers were adequate to determine the presence or absence of an individual on its territory. In many of the instances where marked birds were repeatedly absent from territories, we suspected the bird was dividing his

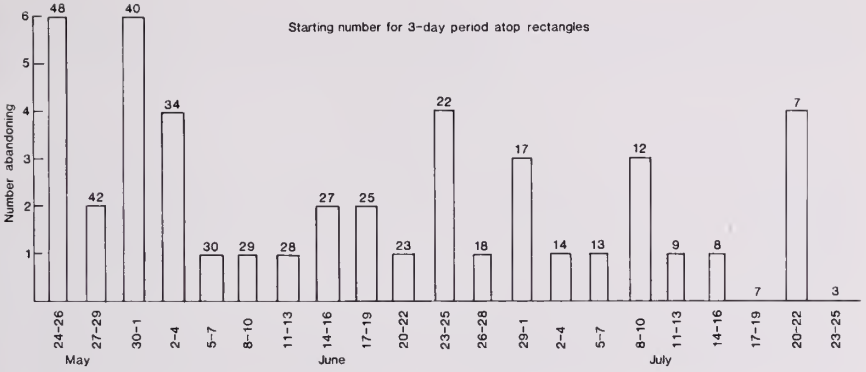

FIG. 1. Number of male Red-winged Blackbirds abandoning roadside territories by 3-day periods, 24 May–25 July 1980.

time between a second (non-roadside) territory and that he may not have been successful in attracting females to nest at either site. We recorded three instances in which males moved from 1–2 km to new roadside territories and were known to have occupied them for 8–14 days. This is too little time to allow production of fledglings from these territories, unless the interloping males displaced males with females already in advanced stages of nesting.

TABLE 3

NESTING STAGES OF FEMALES ON TERRITORIES[a] OF 10 UNMARKED MALE RED-WINGS, CASS COUNTY, NORTH DAKOTA, 24 MAY–25 JULY 1980

Dates	Pre-nest-building	Nest-building and egg-laying	Incubation	Nestlings	Fledglings	Total females seen	Chief activity
24–29 May	—	—	—	—	—	—	nest-building[b]
30 May–5 June	—	—	—	—	—	—	egg-laying[b]
6–12 June	2	4	7	4	1[c]	18	incubation
13–19 June	0	4	4	1	0	9	incubation
20–26 June	1	1	6	2	2	12	incubation
27 June–3 July	0	0	2	7	1	10	feeding nestlings
4–10 July	0	0	2	2	3	7	feeding fledglings
11–17 July	0	0	2	1	2	5	feeding fledglings
18–25 July	0	0	0	0	2	2	feeding fledglings

[a] Different territories selected each week.
[b] From incidental observations.
[c] First fledgling banded on 10 June.

TABLE 4

PERCENT OF ROADSIDE MALE RED-WINGS HOLDING TERRITORIES ON 1 JULY 1980 NOT RESPONDING TO TERRITORIAL TRESPASS, 28 MAY–6 JUNE 1980, CASS COUNTY, NORTH DAKOTA

Territorial males (N = 18)	No.	% observations
Observations	720	—
On territory	642	89.2
Off territory	78	10.8
Not responding to 3-min trespass on territory	60[a]	8.3

[a] Seventeen from sunrise–10:00, 16 from 10:00–13:00, 17 from 15:00–18:00, and 10 from 18:00–sunset.

Some additional aspects of the behavior of breeding males which we learned about through the use of transmitters may affect censusing, and have not, to our knowledge, been reported before. On the evening of 24 May, five instrumented males, which had occupied and contested for territories only minutes before, roosted in a small cattail (*Typha* sp.) marsh 200–600 m from their territories. This marsh was occupied by about 200 breeding Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) during daylight hours. One week later, several of these instrumented males roosted on the territories on which they were marked.

In late May, some unmarked adult males occupied territories just as soon as marked males left them to feed at points at least several hundred meters distant. This usurping activity often occurred at about 10:00 after females had completed nest-building or egg-laying activities for the day. Sometimes within minutes, an unmarked male was seen to alight on the same perch just vacated by the marked male. If not for the marker, one would have assumed that it was the same male. This behavior may partially explain the slightly lower territory occupancy by males during the 10:00–13:00 period in our study, and may present special problems with the Hewitt (1967) sight-capture/sight-recapture census method. Perhaps the most important information obtainable from censuses is the determination of productive territories, and in this regard, the replacement is as predictive as the owner. Thus, inclusion of the 10:00–13:00 period in our analyses appears to have few detrimental influences on our results.

Findings applicable to censusing non-roadside habitat.—For 60 (8.3%) of 720 observations, made from 28 May–6 June, the 18 males that were still holding territories on 1 July did not respond to a 3-min trespass by an observer on their territory and were probably feeding off territory at the time (Table 4). Males still holding territories on 1 July were the ones

most likely to have had females that produced fledglings. Thus, it appears that feeding adult males must be counted when making non-roadside censuses to obtain a complete census.

SUMMARY

Marked territorial male Red-winged Blackbirds (*Agelaius phoeniceus*) were censused on a 30.6-km roadside route in Cass County, North Dakota from 23 May–25 July 1980 to determine the proportion observed during the most favorable daily and seasonal time periods for surveys. We found that censuses conducted in early morning and late afternoon in early June were the most reliable; 80.0% (±SE 1.4%) of territorial males were seen at this time. Numbers of territorial males decreased steadily until early June, when most female redwings were incubating and feeding nestlings. Most (65.8%) of the territorial males missed during censuses were off their territory. Radio transmitter information indicated that territorial males in late May sometimes roosted communally, and that unmarked adult males often quickly replaced the owner of the territory after he left to feed.

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GENERAL NOTES

Wilson Bull., 96(1), 1984, pp. 91–99

Song variation and species discrimination in Blue-winged Warblers.—The ranges of Blue-winged (*Vermivora pinus*) and Golden-winged (*Vermivora chrysoptera*) warblers overlap extensively in the northeastern United States, and hybridization occurs frequently in areas of sympatry (Short, pp. 147–160 *in* Proc. 13th Internatl. Ornithol. Congr., Ithaca, New York, 1963). Information on singing behavior and interspecific discrimination of song has been obtained from populations of these two species in sympatry (Gill and Lanyon, Auk 81:53–64, 1964; Ficken and Ficken, Behaviour 28:149–181, 1967; Ficken and Ficken, Evolution 22:166–179, 1968a; Gill and Murray, Auk 89:625–643, 1972a; Gill and Murray, Evolution 26:282–293, 1972b; Murray and Gill, Wilson Bull. 88:231–254, 1976; Confer and Knapp, Kingbird 27:181–190, 1977), as well as from allopatric populations of blue-wings (Gill and Lanyon, 1964, Lanyon and Gill, Am. Mus. Novit. No. 2176, 1964; Ficken and Ficken, Wilson Bull. 81:69–74, 1969) and golden-wings (Ficken and Ficken 1969; Ficken and Ficken, Behaviour 46:114–128, 1973).

Both species have two song types, designated by Lanyon and Gill (1964) as Type I and Type II; the function of the two song types is uncertain. Both elicit a territorial response from males during playback experiments (Gill and Lanyon 1964; Ficken and Ficken 1969, 1973; Gill and Murray 1972b). Type I may also function in mate selection, but Type II usually is heard later in the breeding season, or after a territorial encounter has been initiated (Ficken and Ficken 1967; Ficken and Ficken, Wilson Bull. 80:442–451, 1968b; Gill and Murray 1972b). Kroodsma (Auk 98:743–751, 1981) provides evidence that local dialects exist in Type II song, but not in Type I song. Four basic components of blue-wing song have been described by Lanyon and Gill (1964) and Gill and Murray (1972b). Lanyon and Gill (1964) present evidence that Blue-winged Warblers from a Long Island population outside the range of golden-wings, exhibit much individual variation in the sequence and number of song components. Blue-winged Warblers in Michigan that are sympatric with Golden-winged Warblers have less variable songs (Gill and Murray 1972a).

Playback experiments have revealed that Blue-winged Warblers which live in sympatry with Golden-winged Warblers discriminate between blue-wing and golden-wing Type I songs better than do allopatric blue-wings (Gill and Lanyon 1964, Gill and Murray 1972b, Murray and Gill 1976). Discrimination between Type II songs of the two species is weak in both sympatry (Gill and Murray 1972b) and allopatry (Gill and Lanyon 1964). Gill and Murray (1972b) suggested that the reduced song variation in sympatric populations may have evolved to facilitate better interspecific discrimination, thus reducing the frequency of interspecific male-female sexual interaction, interspecific male-male aggressive encounters, or both. Alternatively, they note that differences between the sympatric Michigan populations and the allopatric Long Island population may result from chance divergence during allopatry, rather than an adaptive response to the presence of golden-wings in sympatry. My study was designed to distinguish between these alternatives.

Methods.—I studied seven New Jersey populations of Blue-winged Warblers daily, unless there was heavy rain, from 6 May–12 June 1980. I visited the populations on a rotating schedule to avoid biases which may result from comparisons at different stages of the breeding cycle. The study areas included one sympatric population of blue-wings and golden-wings near Waterloo Village (Morris County), and four allopatric populations of blue-wings: Hutcheson Memorial Forest (Somerset County), the Rutgers Ecological Preserve (Middlesex County), Herrontown Woods (Mercer County), and the Princeton Wildlife Refuge (Mercer County) (Fig. 1). Blue-wings and hybrids were present until 1980 in two other study areas,

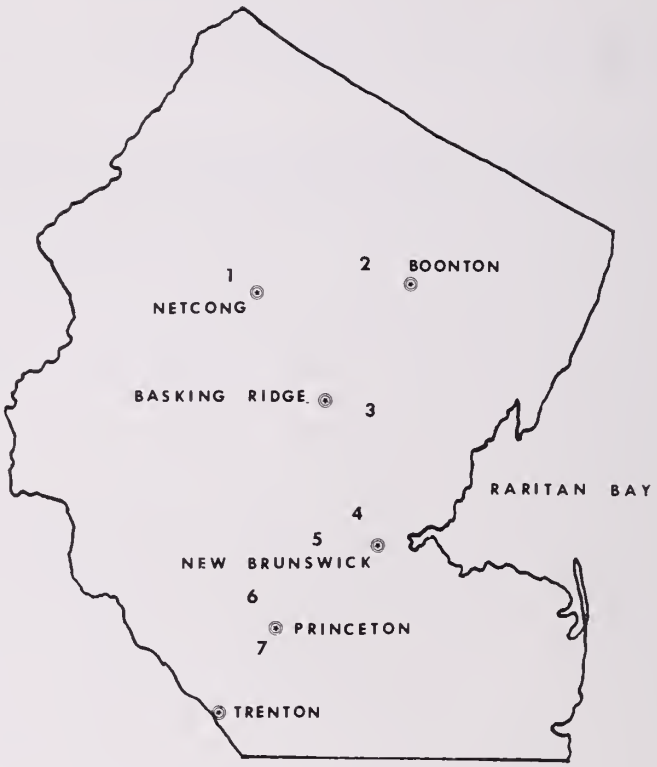

FIG. 1. New Jersey study areas. Number one represents the sympatric population; 2–3 represent the populations with hybrids; 4–7 represent allopatric populations.

located at the Great Swamp Wildlife Refuge and Troy Meadows (both in Morris County). The presence of hybrids in these two populations indicates that at least some of the individuals in the populations had had prior contact with Golden-winged Warblers, and that perhaps ancestors of the entire populations were sympatric with golden-wings at some time in the past. Throughout this paper, I will always refer to the Great Swamp and Troy Meadows as populations with hybrids, in order to maintain a distinction between them and the allopatric populations.

Based on an examination of museum specimens and historical records, Gill (Auk 97:1–18, 1980) hypothesized that Blue-winged Warblers became established in northcentral New Jersey approximately 50 years ago. The breeding range of the Golden-winged Warbler extends north of New Jersey, with a southern extension that coincides with the Appalachian Plateau (A.O.U. Check-list Committee, Checklist of North American Birds, 5th ed., Port City Press, Baltimore, Maryland, 1957). The sympatric study population and the two study populations with hybrids are located in or near northwestern New Jersey, which is part of

TABLE 1
PLAYBACK RESPONSE CATEGORIES AND SCORES

Response	Description	Score
Immediate	Approach to within 10 m of the playback area within the first six renditions	6
Delayed	Approach to within 10 m of the playback area after the first six renditions	3
Complete	Response continues throughout the 15 renditions	4
Active	Constant flitting about the playback area or the flicking of wings and tail of a perched bird	2
Study	Sitting almost motionless within 3 m of the tape recorder with occasional low-intensity vocalizations	2
Passes	Direct flight over the playback area	2
Silence	—	1
Muted song	—	1
Song resumption	Resumption of full song following termination of playback	2

the Appalachian Plateau. I found no record of golden-wings or hybrids breeding elsewhere in New Jersey. Although it is possible that Golden-winged Warblers have bred in areas where the four allopatric study populations of blue-wings are located, available evidence suggests that it is unlikely.

I tape recorded 574 Type I songs from 39 male blue-wings in the field, using a Uher 4000 Report IC tape recorder and a Bell and Howell directional microphone. I analyzed 234 songs (six per individual, in most cases) on a Kay Elemetrics Company Sonagraph Model 6061A. To determine the amount of individual variation, I measured the deviation about the central frequency and modulation rate of each song component. As defined by Greenewalt (Bird Song: Acoustics and Physiology, Smithsonian Institute Press, Washington, D.C., 1968) and modified by Gill and Murray (1972a), "central frequency" refers to the midpoint in the vertical distribution of energy shown on a spectrogram, and "deviation about the central frequency" refers to the range (i.e., the top and bottom points) of vertical energy distribution on a spectrogram.

I tested interspecific discrimination of song by performing playback experiments, similar to those performed by Gill and Murray (1972b). Individual males that sang Type I song within 60 m of the playback area were tested. Fifteen renditions of heterospecific song were played at 10-sec intervals, followed by 15 renditions of homospecific song. If there was a response to heterospecific song, the playback of homospecific song was delayed 10 min. If there was no response to heterospecific song, the homospecific song was played immediately. Responses were scored as described by Gill and Murray (1972b), and are summarized in Table 1. Seventeen was the maximum possible score. A response was considered "strong" if the total score of an individual was greater than 12, and "weak" if the total score was 12 or less. Individuals were placed in one of the following categories: (1) no response (no

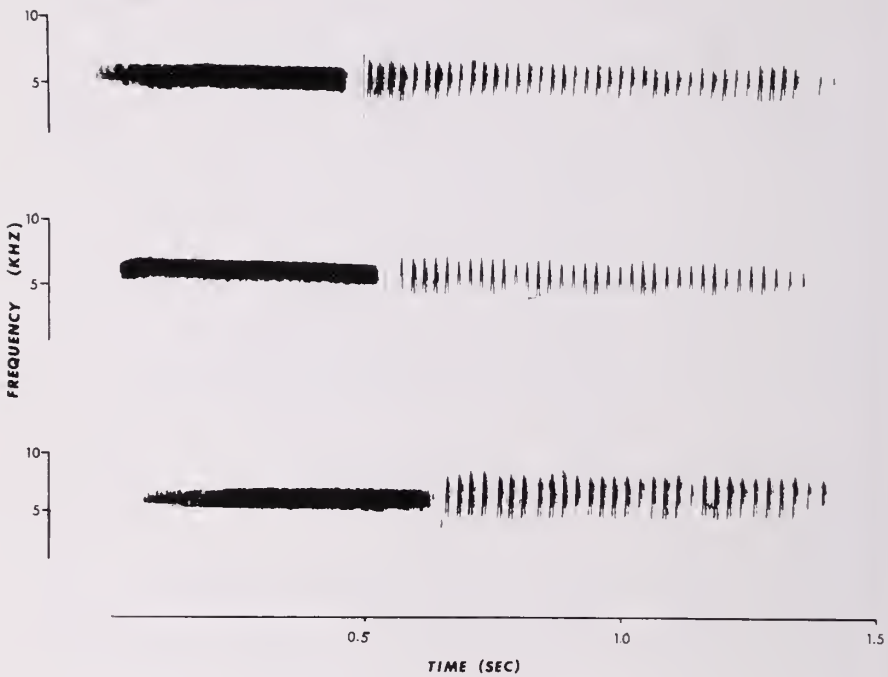

FIG. 2. Typical Type I songs (A-B Pattern) of Blue-winged Warblers. Top: recorded in a sympatric population; Middle: recorded in a population with hybrids; Bottom: recorded in an allopatric population.

response to heterospecific song); (2) weak response (weak response to heterospecific song); and (3) strong response (strong response to heterospecific song). Individuals that did not respond to homospecific song were not included in the analysis.

Results.—Thirty-six of 39 New Jersey blue-wings sang a typical A-B Song Type I (Fig. 2). Slight variation among males within a population occurs in modulation rate and deviation about the central frequency (Table 2). Since modulation rate usually varies within an individual song, I have presented high and low values which represent the range of variability. *F*-tests for homogeneity of variance revealed no significant differences among population types in these parameters (Table 2, $P > 0.10$ in all cases). The three aberrant songs (Fig. 3) were not associated with a particular population type. One was recorded from an individual in the sympatric population, and two were recorded from individuals in two different allopatric populations.

The seven New Jersey populations of Blue-winged Warblers exhibit less population variation in the number and sequence of song components, than was found in the allopatric Long Island population (Fig. 2; Lanyon and Gill 1964). The population variation in number and sequence of song components, deviation about central frequency, and modulation rate in all New Jersey populations is low and similar to the variation observed in Michigan populations (Table 2). *F*-tests for homogeneity of variance revealed significant differences

TABLE 2

VARIATION AMONG POPULATION TYPES IN TYPE I SONGS (A-B PATTERN) OF BLUE-WINGED WARBLERS

Song parameter	Population type			
	Michigan[a]	New Jersey		
	Sympatric (N = 16)	Sympatric (N = 7)	With hybrids (N = 13)	Allopatric (N = 19)
Component A				
MRL[b] (Hz)	229.4 ± 10.71 (4.0)[c]	230.0 ± 8.16 (3.6)	243.1 ± 12.51 (5.2)	235.5 ± 12.34 (5.2)
MRH (Hz)	242.5 ± 7.75 (3.0)	264.3 ± 7.87 (3.0)	265.4 ± 9.67 (3.7)	260.0 ± 10.26 (4.0)
FRL (kHz)	5.1 ± 0.25 (5.1)	4.3 ± 0.39 (9.2)	4.8 ± 0.39 (8.1)	4.6 ± 0.36 (7.7)
FRH (kHz)	7.1 ± 0.20 (2.9)	7.4 ± 0.38 (5.1)	7.5 ± 0.41 (5.4)	7.3 ± 0.57 (7.8)
Component B				
MRL (Hz)	44.0 ± 3.87 (8.9)	40.0 ± 0.00	40.8 ± 2.77 (6.8)	39.8 ± 1.12 (2.8)
MRH (Hz)	44.3 ± 4.17 (9.4)	45.7 ± 5.35 (11.7)	46.9 ± 4.80 (10.2)	45.0 ± 5.13 (11.4)
FRL (kHz)	3.7 ± 0.80 (21.4)	2.7 ± 0.39 (14.5)	2.9 ± 0.34 (11.8)	2.7 ± 0.49 (18.5)
FRH (kHz)	8.3 ± 0.46 (5.5)	8.7 ± 0.27 (3.1)	8.5 ± 0.43 (5.1)	8.7 ± 0.46 (5.3)

[a] Gill and Murray (1972a).
[b] MRL and MRH represent low and high extremes of the range of modulation rates. FRL and FRH represent low and high extremes of deviation about the central frequency.
[c] $\bar{x}$ ± SD (coefficient of variation).

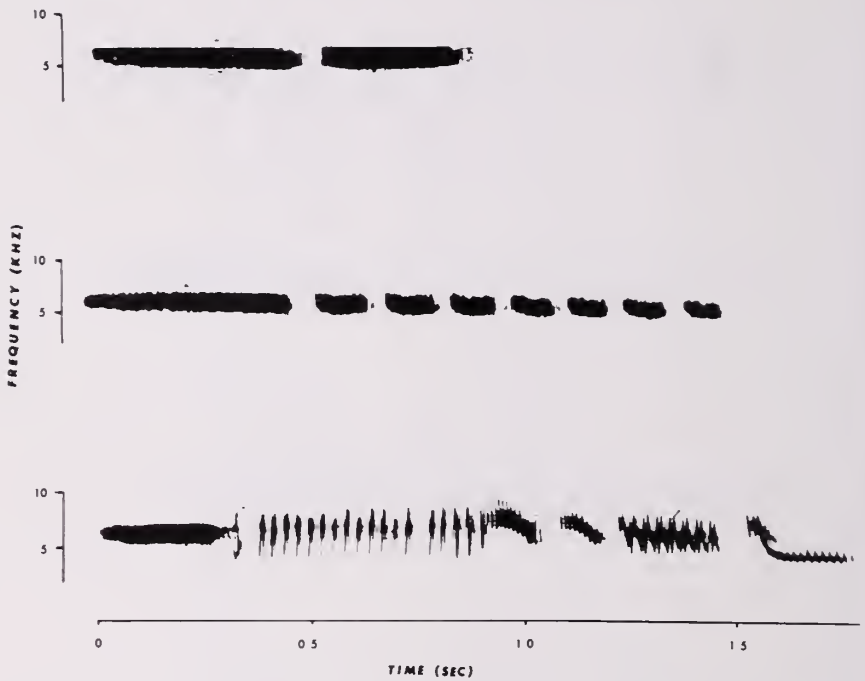

FIG. 3. Aberrant Type I songs of Blue-winged Warblers. Top and Bottom: recorded in allopatric populations; Middle: recorded in a sympatric population.

in only 3 of 24 comparisons between Michigan and New Jersey ($P < 0.05$, in all three cases): component A FRH was less variable in sympatric Michigan populations than in allopatric New Jersey populations; component B MRL was more variable in sympatric Michigan populations than in allopatric New Jersey populations; and component B FRL was more variable in sympatric Michigan populations than in New Jersey populations with hybrids. (Deviation about the central frequency and modulation rate were not measured in the Long Island songs.)

The behaviors of blue-wing males that responded strongly to the experimental playback of heterospecific song was similar to their behavioral responses to playback of homospecific song. A strong response usually included an immediate approach to the playback area, active behavior (a constant flitting about the experimental area or the flicking of wings and tail of a perched bird), direct flights over the tape recorder, silence or muted song, and resumption of full song after playback. The behavior of blue-wing males that responded weakly to heterospecific song differed not only in intensity but in quality. In 10 of the 13 cases of weak response, the warbler approached to within 10 m of the tape recorder during the first six renditions of playback, and sang throughout the experiment. The song was not muted or altered in any obvious way. Active behavior and flights over the tape recorder did not occur. Shortly after termination of playback, the male flew farther away and continued to sing.

Blue-winged Warblers sympatric with Golden-winged Warblers discriminated between blue-wing and golden-wing Type I songs more often than did Blue-winged Warblers from

TABLE 3
RESPONSES OF TERRITORIAL MALE BLUE-WINGED WARBLERS TO EXPERIMENTAL PLAYBACK OF GOLDEN-WINGED WARBLER SONG TYPE I

	No response	Weak response	Strong response	Total
Sympatric	4	2	0	6
With hybrids	4	3	2	9
Allopatric	5	8	4	17

allopatric populations; Blue-winged Warblers from populations with hybrids discriminated between blue-wing and golden-wing Type I songs more often than did blue-wings in areas where neither golden-wings nor hybrids have probably ever bred (Table 3, $\chi^2 = 12.65$, df = 1, $P < 0.005$).

Discussion.—Interspecific hybridization is expected to be maladaptive, occasionally acting as a selective pressure favoring increased premating behavioral isolation (Dobzhansky, Genetics of the Evolutionary Process, Columbia Univ. Press, New York, New York, 1970). Interspecific aggression is always maladaptive in a subordinate species and may be maladaptive in a dominant species, whether or not it is a result of misdirected intraspecific aggression (Murray, Ecology 52:414–423, 1971; Biol. Rev. 56:1–22, 1981). Therefore, factors which promote species discrimination would be favored in situations where either hybridization or maladaptive interspecific aggression is likely to occur. Similar reasoning is implicit in Gill and Murray's (1972b) hypothesis that reduced song variation observed in sympatric populations of Blue-winged and Golden-winged warblers in Michigan may have evolved to facilitate the increased interspecific discrimination observed in the same populations, relative to an allopatric population on Long Island (Gill and Lanyon 1964, Lanyon and Gill 1964). My data appear to be inconsistent with this hypothesis, as well as with an alternative hypothesis that the observed differences between Michigan and Long Island may result from geographic variation, rather than as an adaptive response to the presence of golden-wings.

The interpretation of the results concerning song variation in New Jersey populations depends on whether or not golden-wings were sympatric with the four allopatric populations of blue-wings at some time in the past. If golden-wings and blue-wings were previously sympatric throughout New Jersey, then the low amount of song variation could be interpreted as the result of selection to facilitate interspecific discrimination. If golden-wings have never bred in the four allopatric study areas (which available evidence suggests [A.O.U. Checklist 1957]), then the absence of consistent differences correlated with allopatry or sympatry among the New Jersey populations suggests that there has been no selection for reduced variability. The apparent absence of such effects could indicate either the absence of a significant selective pressure or that the amount of variability in song was insufficient for selection to operate. Considering the close proximity of New Jersey and Long Island, it is surprising that song characters in the New Jersey populations examined are more similar to song in Michigan populations. This suggests that the variation in Long Island song cannot be explained simply as geographic variation. The low amount of variation in allopatric New Jersey populations also indicates that the variation in Long Island song cannot be attributed to an absence or relaxation of stabilizing selection owing to an absence of Golden-winged Warblers. Further research will be necessary to determine why blue-wing songs on Long Island are so variable.

Although there is no difference in song variation among the New Jersey populations, Blue-winged Warblers that are sympatric with Golden-winged Warblers discriminate between heterospecific and homospecific song more often than do Blue-winged Warblers from allopatric populations (Table 3). Greater discrimination could result from selection to reduce the probability of hybridization, interspecific aggression, or both. Since only males respond to playback experiments, it is not possible to determine whether or not females follow the same trend in discrimination ability. Therefore, it is not possible to distinguish between the two selection pressures.

The greater discrimination observed in sympatric New Jersey populations could be genetically determined or learned. However, selection for genetically determined discrimination ability probably has not occurred in the New Jersey populations. Given the presence of hybrids at the Great Swamp and Troy Meadows, it is reasonable to assume that recent ancestors of many individuals in these populations had contact with golden-wings, hybrids, or both. If this assumption is correct, and if genetically determined discriminatory ability had been selected, individuals in these populations would be expected to discriminate as well as individuals from the sympatric population, because selection pressures probably would not have relaxed for sufficient time to produce a noticeable genetic change.

Gill and Murray (1972b) and Murray and Gill (1976) suggested a more plausible explanation for differences in discrimination ability based on learning. Blue-winged Warblers sympatric with Golden-winged Warblers could habituate (i.e., cease to respond) to interspecific song owing to a lack of appropriate visual stimuli. This does not require that the species be sympatric for a long period. The two populations with hybrids provide evidence for this hypothesis because they contain an intermediate number of discriminators. An intermediate number of discriminators could result if: (1) older birds learned to discriminate in previous years when there may have been greater numbers of golden-wing or hybrid models, while younger birds did not learn to discriminate because of fewer models or (2) the number of models in these populations has been consistently fewer than the number of models in the sympatric population, and only those blue-wings which had frequent contact with golden-wings or hybrids (e.g., neighbors with adjacent or overlapping territories) learned to discriminate.

In general, behavior patterns are triggered by any one of a broad range of stimuli. However, the intensity of the response will vary with stimulus intensity and quality. There is usually an "optimal" stimulus which will elicit the strongest response. For example, Curio (Animal Behaviour 23:1–115, 1975) has shown that the form and intensity of mobbing vary with the similarity between an experimental stimulus and an actual predator. Similarly, Blue-winged Warblers exhibit varying responses to a broad range of auditory stimuli. A typical Blue-winged Warbler in an allopatric population will respond by approaching a song of buzzy quality. Yet, the quality and intensity of the response to a golden-wing song differ from those exhibited in response to the optimal stimulus, blue-wing song. Inexperienced individuals in sympatric populations may show the same response. However, experience with golden-wings may eliminate the response by reducing the probability of responding to the sub-optimal stimulus of golden-wing song. Murray and Gill (1976) reported anecdotal evidence consistent with this view. A Blue-winged Warbler in a sympatric population initially responded aggressively to the song but not the plumage of a Golden-winged Warbler, that sang a blue-wing Type I song. Eventually, the response waned, although the individual continued to respond to other blue-wing songs, when associated with the appropriate visual stimuli.

A similar example of learning to modify a behavioral response based on an interaction between visual and auditory stimuli was reported by Rice (Wilson Bull. 93:383–390, 1981), who observed responses of Red-eyed Vireos (*Vireo olivaceous*) to a conspecific male which

sang an aberrant song. Vireos which held territories distant to the aberrant individual ignored playback of the aberrant song, as if they did not recognize it as the song of a conspecific. However, the four immediate neighbors of the bird reacted to its song no differently than they reacted to normal song. Apparently the neighbors of this individual learned to respond to the unusual song because it was associated with the appropriate visual stimuli. The learning hypothesis could be tested by using models during playback experiments. If it is true, birds in allopatric populations should habituate to golden-wing song if it is presented simultaneously with a golden-wing model, but should not habituate if presented with a blue-wing model.

If it is adaptive for Blue-winged Warblers to discriminate between species (to reduce the frequency of hybridization, interspecific aggression or both), then the learning mechanism described here is probably more efficient than selection for a genetically determined response. Because selection for a genetically determined response involves a change in gene frequencies which varies with each situation, it requires more time and involves waste in maladapted offspring, whereas learning involves a rapid response to different environmental conditions and offers individuals immediate advantages (Shields, Philopatry, Inbreeding, and the Evolution of Sex, State Univ. of New York Press, Albany, New York, 1982).

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The songs of *Microcerculus* wrens in Costa Rica.—The starting point of my recently published study of the taxonomy of *Microcerculus* in Middle America (Stiles 1983, Wilson Bull. 95:169–183) was the existence of two strikingly different "song types" in Costa Rica, as was first recognized by Slud (1958, Condor 60:243–251). Morphological and distributional data led me to conclude that the song types in reality represented different species, the northern *M. philomela* (Nightingale Wren) and the southern *M.* (*marginatus*?) *luscinia* (Whistler Wren). In the course of this study, I also recorded both song types, but unfortunately the sonograms reached me just too late to be included in the paper. Accordingly I present here descriptions and sonograms of representative songs of the two species of *Microcerculus* wrens in Costa Rica and briefly compared them with songs of other populations of these species, other *Microcerculus,* and other genera of wrens. Songs were recorded on a Uher 4000-L tape recorder with an M-517 Uher microphone and a Griffith fiberglass parabolic reflector.

The song of *M. philomela* (Fig. 1) consists of a long series of pure clear whistles, mostly without harmonics, that are given at a rate of ca. 2 per sec. The whistles are 0.3–0.4 sec in duration, and even-pitched or upslurred at frequencies between 3 and 6 kHz. Successive notes are typically on different pitches, such that the song "rises and falls in an arresting manner" (Slud 1958). The overall effect is sometimes strikingly tuneful, and was undoubtedly

FIG. 1. A complete song of *Microcerculus philomela* recorded at Finca La Selva, Sarapiquí, Prov. Heredia, Costa Rica, on 26 Feb. 1981. Note the opening motif of shorter, softer, more rapid notes, and the tendency of the main part of the song to break into "phrases" of 6–8 notes.

responsible for the vernacular name of "nightingale" wren (although it certainly does not resemble the song of the true nightingales [*Luscinia* spp.]). The duration of the song is quite variable, ranging from less than 10 to over 20 sec. The main part of the song is introduced by a series of shorter, softer, more rapid notes. This opening motif is quite variable, and may consist of up to 10 notes (pers. obs.). I have heard the same bird give longer or shorter opening motifs on successive songs.

The song of *M. luscinia* shows some similarity in the form of the individual notes, but its structure is almost totally different (Fig. 2). The song opens with a series of ca. 10–15 short notes that decelerate, lengthen, increase in loudness, and rise in pitch from ca. 4.5 to over 5 kHz. The number of notes in this opening motif varies from ca. 8–14 in the three songs recorded (the first notes are so soft and fast that they are difficult to count and may easily be lost from the recording). The opening motif is followed by two loud, upslurred notes (7–8 kHz) that resemble in structure some of the notes in the song of *M. philomela*.

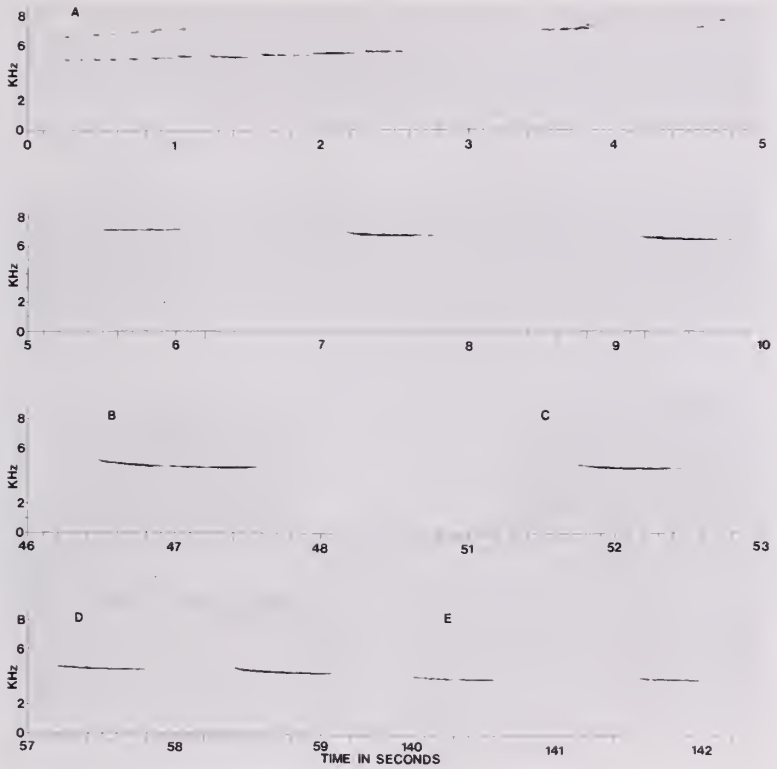

FIG. 2. Selected portions of a song of *Microcerculus luscinia,* recorded at Finca "Los Cusingos," El Quizarrá, Prov. San José, on 17 June 1982. See text for a description of the complete song (which would have required some 20 m of sonograms to display!). A. Opening motif through the first three single whistles; B. next-to-last single whistle; C. last single whistle; D. first double whistle; E. last double whistle.

From here on, however, the song is totally different. First there follows a series of pure, long-drawn-out, high-pitched whistles, which gradually become longer, more slurred, lower-pitched, and widely spaced through the series. The first whistles in the series are ca. 0.8–0.9 sec in duration, at a frequency of ca. 6.8 kHz little slurring, and separated by an interval of ca. 1 sec; the last ones slur from 5 to ca. 4.5 kHz, last 1.4–1.5 sec, and are separated by intervals of ca. 3.8 sec. In the three songs recorded, the number of single whistles is 13 or 14. Then, following a gap of ca. 4 sec, there begins a series of double whistles. The commonest notes are each ca. 1 sec in length and separated by 0.4–0.5 sec; the interval between doubles increases gradually from ca. 3.8 sec at the start, to ca. 5 sec at the end of the sequence. The first note of each double is distinctly downslurred, the second only slightly so; the frequency

of successive doubles gradually declines from 5–4.5, to slightly less than 4 kHz through the series. In all, some 15–18 doubles occurred in the three recorded songs although I have heard songs with as few as five (possibly interrupted) and as many as 20 or more, with the intervals between doubles increasing to 6–8 sec in the longest songs. The three full songs recorded averaged ca. 2.5 min in length, most of which (1.5 min or more) was occupied by the final sequence of double whistles (Fig. 2).

The opening motifs of both *M. philomela* and *M. luscinia* consist of softer and more rapid notes. In both species I have encountered considerable variability in the number and rapidity of these notes both between individuals and different songs of the same individual. It is my strong subjective impression that sometimes the opening motifs of the two species can be quite similar. Unfortunately, I lack a wide enough selection of recordings (or sonograms) to verify this impression. Aside from this variation in the opening motif, and in total song length, I have encountered no striking variation between the songs sung by a given individual: each individual seems to have but a single song.

I have also detected considerable geographic variation in the songs of both forms. In *M. philomela,* the La Selva song (shown in Fig. 1) is to me the most strikingly melodious, showing a tendency to break into "lines" of ca. 6–8 notes. In other populations, the song is often less strikingly melodious, with a less defined cadence; however, in all the delivery rate of ca. two notes per sec is preserved and the length of the individual notes is similar. Total length of the song seems to vary at least as much within as between most populations, although all songs heard at one locality, Volcán Orosí, in northern Costa Rica, were quite short (ca. 7–10 sec). A song of *philomela* recorded in Chiapas, Mexico (Hardy 1978, "The Wrens," ARA Records, no. 2) is structurally identical to those of Costa Rican birds, including the opening motif, but is longer than most.

In *M. luscinia,* variation is most evident in the last part of the song, specifically whether it is composed of single or double notes. Most populations on the Pacific slope of Costa Rica end the song with a long series of double notes; on the Atlantic slope, these final notes are single: there is no transition in the middle of the song, but the whistles and the intervals between them lengthen gradually throughout the song. One song I listened to at Bribrí, near the Panama border, lasted nearly 4 min; the interval between successive whistles was at least 12 sec at the end. A song of *M. m. marginatus* from NE Peru (Hardy 1978) seems very similar in temporal structure to the single-note version of the song of *luscinia.* However, the song as presented on the record is considerably shorter than a typical one of *luscinia,* and lacks the opening motif. I suspect that the recorded song is incomplete: given the length of the song and the usually long intervals between songs, it is all too easy to break into the middle of a song, and frustratingly difficult to record the opening motif! If a complete song of *marginatus* is indeed longer and with a fast, soft opening motif, this would provide strong support for considering *luscinia* as a subspecies of *marginatus.*

This geographical variation in no way blurs the distinctness of the two song types: there is always an order-of-magnitude difference in delivery rate, and the individual notes in the song of *luscinia* are always 2–4 times longer than those in the song of *philomela.* The birds themselves seem unequivocal in recognizing the difference, as well. My whistled renditions of the La Selva song type consistently produce strong reactions (countersinging and close approach) in other *philomela* populations (e.g., Carrillo, Volcán Orosí, Bijagua), but never in *luscinia* populations (Quizarrá, Osa Peninsula, vic. Parrita). On the other hand, a very poor-quality recording of a *luscinia* song from Bribrí evoked a strong reaction from birds of Golfito and the General Valley, on the southern Pacific slope, but was ignored by La Selva birds. I should emphasize that my sample sizes for these "experiments" are small, and that a much larger number of recordings and experiments would be required to evaluate

the importance of geographic variation within song types, as well as my hypothesis that similarity in the opening motifs might facilitate interspecific territoriality (Stiles 1983).

Consisting as they do of pure-toned, unmodulated, long (0.3 sec or more) whistles, the songs of the two Costa Rican species of *Microcerculus* seem ideally suited for transmission in an obstruction-filled habitat like tropical forest understory (Morton 1975, Am. Nat. 109:17–33). Other understory wrens (e.g., *Henicorhina, Cyphorhinus*) sing songs of comparable tone quality, as do the other two recognized species of *Microcerculus, bambla* and *ustulatus* (cf. Hardy 1978). The songs of the latter two species have a very different temporal structure, however, with the whistles becoming progressively shorter and more rapid (in *ustulatus,* but not in *bambla,* the song finishes as an up- or down-slurred glissando). Of the wide selection of wren songs presented by Hardy (1978), that of *Cyphorhinus aradus* is most comparable in tone quality to those of *Microcerculus,* but is very different structurally: a low, burbling phrase is interspersed with the clear whistles, which themselves are given in a seemingly random order quite unlike the patterned utterances of *Microcerculus* spp. Thus, although song tends to confirm that the species of *Microcerculus* form a natural unit, it is scarcely helpful in establishing the relationship of this unit to the other genera of wrens.

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Cowbird nest selection.—The Brown-headed Cowbird (*Molothrus ater*) is well known for its brood parasitic habit (Friedmann et al., Smith Contrib. Zool. 235, 1977). The large number of recorded hosts testifies to the variety of situations encountered by egg-laying females. Since cowbird nesting activities are not centered on their own nests, the manner of host selection is an important factor in determining reproductive success of individual females. How, then, do cowbirds select host nests?

If all potential host nests are at equal risk (same probability) of being parasitized, and since cowbird parasitism is a "rare" event, the distribution of 0, 1, 2, 3, . . . cowbird eggs per nest will approximate successive terms of a Poisson series. Preston (Ecology 29:115–116, 1948) tested for such a distribution and found no good statistical fit; however, within the sample of parasitized nests, the distribution of cowbird eggs after the first egg did fit the Poisson distribution that was generated. He concluded that the first cowbird egg in a nest was placed nonrandomly and subsequent, additional eggs were randomly distributed among the already parasitized nests. Mayfield (Condor 67:257–263, 1965) looked at similar data and felt that host nests with one cowbird egg were under represented in the sample. Since some hosts may immediately abandon their nests after the first cowbird egg appears, these abandoned nests become difficult to locate. By adding 10–15% to the number of nests with one cowbird egg, he produced a close fit to Poisson distributions. Mayfield (1965) concluded that cowbirds distribute eggs randomly among available host nests. Elliott (Auk 94:590–

TABLE 1

FIT OF COWBIRD EGG DISTRIBUTION TO AN EXPECTED RANDOM DISTRIBUTION; SEE MAYFIELD (1965) OR ORIGINAL PAPERS FOR DETAILED DISTRIBUTION OF COWBIRD EGGS; FIT IS COMPARED WITH A POISSON DISTRIBUTION CALCULATED USING THE METHODS DESCRIBED IN THE TEXT

Study and source	Total nests S	Nests not found $U(0)$	Nests found, not parasitized $F(0)$	Cowbird eggs E	Parasitized nests $T - F(0)$		Fit to Poisson		
							χ^2	df	P
A. Studies which fit a Poisson distribution									
20 Michigan hosts (Berger, Wilson Bull. 63:26–34, 1951*)	500	349.8	38.2	204	112	1.358	3.10	3	$P > 0.5$
Ovenbird (*Seiurus aurocapillus*; Hann, Wilson Bull. 49:145–237, 1937*)	42	17.0	3.0	40	22	1.600	2.42	2	$P > 0.1$
Kentucky Warbler (*Oporornis formosus*; Jacobs, Auk 55: 260–262, 1938*)	134	16.7	56.3	80	61	0.682	0.97	1	$P > 0.1$
Song Sparrow (*Melospiza melodia*; Nice, Trans. Linn. Soc. N.Y. 4, 1937*)	223	51.8	73.2	129	98	0.754	2.57	1	$P > 0.1$
14 Pennsylvania hosts (Norris, Wilson Bull. 59:83–103, 1947*)	237	121.3	42.7	108	73	0.933	0.62	1	$P > 0.1$
Field Sparrow (*Spizella pusilla*; Walkinshaw, *in* Bent, U.S. Natl. Mus. Bull. 237, pt. 2, 1968*)	664	287.9	194.1	234	182	0.622	2.41	1	$P > 0.1$
Eastern Phoebe (*Sayornis phoebe*; Klaas, Occ. Pap. Mus. Nat. Hist., Univ. Kansas, 41, 1975)	377	210.6	85.4	115	81	0.691	0.68	2	$P > 0.5$
13 Kansas hosts (Hill, Wilson Bull. 88:555–565, 1976)	520	232.0	177.0	144	111	0.500	1.78	1	$P > 0.1$

TABLE 1
CONTINUED

Study and source	Total nests S	Nests not found $U(0)$	Nests found, not parasitized $F(0)$	Cowbird eggs E	Parasitized nests $T - F(0)$	c	Fit to Poisson χ^2	df	P
24 midwest hosts (Lowther, Bird-Banding 48:358–369, 1977)									
	466	289.7	98.3	111	78	0.630	2.17	1	$P > 0.1$
Prairie Warbler (*Dendroica discolor*; Nolan, Orn. Monogr. 26, 1978)									
	336	−2.1	256.8	104	92	0.300	1.97	1	$P > 0.1$
Pooled studies	3499	516.4	930.6	1270	910	0.690	1.33	3	$P > 0.5$
Heterogeneity χ^2							17.36	11	$P = 0.1$
B. Studies which do not fit a Poisson distribution									
3 Kansas hosts (Elliott 1977)									
	72	−5.5	24.5	144	53	1.857	29.64	3	$P < 0.01$
Kirtland Warbler (Mayfield 1960*)									
	137	−18.2	80.2	125	75	0.806	12.21	2	$P < 0.001$
Red-eyed Vireo (Southern 1958*)									
	104	−28.8	57.8	136	75	1.024	12.90	2	$P < 0.001$
Red-winged Blackbird (Linz and Bolin 1982)									
	258	43.5	105.5	182	109	0.848	9.27	2	$P < 0.01$

* Studies used in Mayfield (1965).

593, 1977) felt Mayfield's (1965) correction introduced other uncontrolled biases and he supported Preston's (1948) earlier interpretation.

My approach to examining cowbird egg distribution considers a different sort of bias in the data. I consider parasitism of host nests by female Brown-headed Cowbirds to be a 2-step process: (1) a successful search for a host nest and, (2) selection of the nest from among those nests that have already been found by the cowbird. A nest with a cowbird egg is known to have been found by a cowbird; nests without cowbird eggs either may be known to cowbirds but not selected to be parasitized or may have remained undetected from nest-searching cowbirds.

Of a sample of nests, let the total number of nests, S, be the sum of the series,

$$S = N(0) + N(1) + N(2) + N(3) + \ldots = \sum_{i=0}^{j} N(i),$$

where $N(i)$ is the number of host nests with $i = 0, 1, \ldots, j$ cowbird eggs. Those nests without cowbird eggs, $N(0)$, are of two types:

$U(0)$ = those nests remaining unknown to cowbirds and therefore not exposed to risk of parasitism and, properly, not to be included in the sample (Mayfield, The Kirtland's Warbler, Cranbrook Inst. Sci., Bull. 40, 1960:155; 1965:260); and

$F(0)$ = those nests which had been found by cowbirds but not parasitized.

Randomness of cowbird egg distribution ought to be tested using the series,

$$T = F(0) + N(1) + N(2) + N(3) + \ldots,$$

where T is the total number of nests found by cowbirds. The value of $F(0)$, however, is difficult to know. The Poisson expansion provides a means to overcome this problem. Individual terms of a Poisson series can be expressed as

$$N(i) = c^i T e^{-c}/i!$$

for $i = 0, 1, 2, \ldots, j$ cowbird eggs/nest, and where c = mean number of cowbird eggs/nest for those nests found by cowbirds, e = base of natural logarithms, and $N(i)$ and T as defined above. The ratio of successive terms can be used to provide estimated values of c and T. Using the ratio $N(2)/N(1)$ gives,

$$N(2)/N(1) = (c^2 N e^{-c}/2!)/(cNe^{-c}/1!) = c/2.$$

This equation leads to the equality $c = 2[N(2)/N(1)]$. If the total number of cowbird eggs in the sample is E, and since $c = E/T$ also, T can be found as $T = E/c$. (Because both c and T are derived from the data, an additional 2 degrees of freedom are lost in χ^2 goodness-of-fit testing to the Poisson distribution that is generated. One then uses $m - 3$ (or $j - 2$, j as used above) degrees of freedom where m = number of categories of nests with different numbers of cowbird eggs.)

I used this method to compare cowbird egg distributions reported in several studies (including those used by Mayfield 1965) to Poisson distributions. Most studies showed no significant departure from a Poisson distribution (Table 1). Mayfield's (1965: 260) "most conspicuous deviations from randomness . . . [resulted from] . . . too many nests with no cowbird eggs and too few nests with one cowbird egg." My method assumes some nests were not exposed to parasitism risk and reduces the number of nests with no cowbird eggs. For the 14 studies I examined (Table 1), four cases depart from a Poisson expectation. These studies, with significant departures from randomness, are themselves interesting and relate to the ecology of cowbird-host community interactions. Although the remaining cases seem

to tend towards significance, the pooled data and a heterogeneity χ^2 test (Sokal and Rohlf, Biometry, 2nd ed., W. H. Freeman and Co., San Francisco, California, 1981) do not confirm this tendency. Three exceptions show negative values for $U(0)$—nests not found—which implies that all nests could be found and were exposed to parasitism risk and that the host community was under heavy cowbird pressure. If cowbird parasitism is not a rare event, the Poisson distribution becomes an inappropriate standard to test for a random distribution. These exceptions are discussed below.

Mayfield's (1965) analysis showed cowbird egg distribution among Kirtland Warbler (*Dendroica kirtlandii*) nests barely demonstrated non-significant departure from a Poisson distribution (Mayfield 1965:Table 1). There is a history of heavy cowbird parasitism on this species, a factor contributing to this warbler's endangered status. Apparently Kirtland Warblers' nests are easily found by cowbirds since few other species are victimized in warbler habitat (Harwood, Audubon 83:99–111, 1981). Most cowbird nest finding is done by sit-and-watch activities (Hann, Wilson Bull. 53:211–221, 1941; Norman and Robertson, Auk 92:610–611, 1975) and Kirtland Warbler habitat provides many places for doing just this (Anderson and Storer, Jack-Pine Warbler 54:105–115, 1976).

Southern (Jack-Pine Warbler 36:105–130, 185–207, 1958) described nest-sites of Red-eyed Vireos (*Vireo olivaceus*) as usually near small clearings in woods. Such a location—at a habitat discontinuity—would be at high risk of cowbird parasitism (Gates and Gysel, Ecology 59:871–883, 1978). Nest location, and perhaps observer interference (J. C. Barlow, pers. comm.), may have aided cowbirds in finding these vireo nests.

Elliott's (1977) prairie community consisted of three primary hosts: Eastern Meadowlark (*Sturnella magna*), Dickcissel (*Spiza americana*), and Grasshopper Sparrow (*Ammodramus savannarum*). Most nests were parasitized more than once and many were visited by two or more cowbirds. Kansas supports high densities of cowbirds (Dolbeer and Stehn, F&WS Spec. Sci. Rept., Wildl. No. 214, 1979) and the low diversity of prairie bird communities means relatively few hosts per breeding female cowbird and a resultant high cowbird pressure on the host community (Zimmerman, Auk 99:292–298, 1982; Bull. Ecol. Soc. Am. 63:102, 1982).

Red-winged Blackbirds (*Agelaius phoeniceus*) studied by Linz and Bolin (Wilson Bull. 94: 93–95, 1982) had more unparasitized nests and fewer one- and two-cowbird egg nests than expected. Colonial red-wings are less often parasitized than upland nesting individuals (Friedmann, U.S. Natl. Mus. Bull. 233, 1963) due, in part, to group defense against cowbirds (Folkers, Kansas Ornithol. Soc. Bull. 33:32–34, 1982; Robertson and Norman, Condor 78: 166–173, 1976). The red-wing population studied by Linz and Bolin (1982) was comprised of birds nesting in cattails along roadside ditches. My analysis suggests that most of these red-wing nests were well defended and under low cowbird pressure (i.e., many nests with no cowbird eggs and few nests with only one cowbird egg). Those nests that were parasitized were parasitized more than once, suggesting that cowbirds were not prevented from visiting them.

Other examples in Table 1 do not show significant departure from a Poisson distribution. This collection of single-host and multi-host studies show a random distribution of cowbird eggs. Female cowbirds are likely opportunists in host selection. Some nests are never exposed to parasitism risk but all others have equal likelihood of being parasitized. Host communities with much cowbird pressure seem exceptions to such a random egg distribution.

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Niche relationships in wintering mixed-species flocks in western Washington.—Mixed-species flocks are common worldwide. Study of these flocks has focused on two major questions: (1) What are the functions of mixed flocks? and (2) What is the importance of interspecific competition within these flocks? It is generally agreed that members of mixed-species flocks may derive benefits of increased foraging efficiency and decreased risk of predation, although the importance of each potential benefit may vary among species or geographical regions (for review see Morse, Bioscience 27:332–339, 1977). The dilemma of interspecific competition within mixed flocks has not been resolved. Many authors have argued that competition is avoided or reduced by species differences in foraging behavior (e.g., Gibb, Ibis 96:513–543, 1954; Austin and Smith, Condor 74:17–24, 1972). Evidence of species differences and/or low niche overlap alone, however, cannot conclusively demonstrate the importance of competition because overlap can assume a variety of levels if resources are not limiting (Sale, Oecologia 17:245–256, 1974).

We studied wintering mixed flocks of insectivorous birds in western Washington to determine: (1) mixed flock characteristics (e.g., species composition, flock size, etc.); (2) the frequency of aggressive encounters (intra- and interspecific) within mixed flocks; and (3) differences in foraging niches of species which regularly participated in mixed flocks (core species). In this report we compare our data with those of Morse (Ecol. Monogr. 40:119–168, 1970; Ibis 120:298–312, 1978) from other north-temperate study sites. Western Washington differs from other study regions in climate, habitat, and the species composition of mixed flocks. Taken as a whole, differences among sites in the parameters examined may provide insight into the competitive relationships within mixed flocks.

Study area and methods.—We conducted this study at the Nisqually National Wildlife Refuge, Thurston Co., Washington. Data were collected along a 3-km wooded dike bordering the Nisqually River. Red alder (*Alnus rubra*) dominated the mature deciduous woodland. Big-leaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*), and Oregon ash (*Fraxinus latifolia*) were also common canopy species. Most canopy trees were approximately 25 m tall. Understory species included wild crabapple (*Pyrus fusca*), elderberry (*Sambucus* sp.), blackberry (*Rubus* sp.), Indian peach (*Oemleria cerasiformis*), salmonberry (*Rubus spectabilis*), willow (*Salix* sp.), and snowberry (*Symphoricarpus albus*). Data collection was facilitated because flocks were usually restricted to this narrow band of woodland.

To minimize possible seasonal variation, we collected data from 8 January–13 February 1975. Observations were made between 11:00 and 14:00 approximately 3 days each week. Flock composition and size were determined upon encountering the flock. A flock was operationally defined as two or more individuals travelling and foraging together. Fifteen-second focal-animal samples (Altmann, Behaviour 49:227–267, 1974) were taken of as many flock members as possible. Data were dictated into a cassette recorder and included: (1) number of foraging motions (captures and/or capture attempts); (2) type of foraging behavior used for each foraging motion; and (3) location where foraging motions occurred (microhabitat). Foraging behavior classification, modified from Sturman (Condor 70:307–322, 1968), was based on stance (upright, hang, and fly), and method (glean, peck, tear, and flycatch). Fourteen microhabitats were defined according to structural, vertical, and horizontal components (Fig. 1). These factors seemed appropriate for quantifying foraging niche in view of previous mixed-flock studies (e.g., Ulfstrand, Oecologia 27:23–45, 1977; Austin and Smith 1972; Morse 1970, 1978). Data were analyzed using the Statistical Analysis System (Helwig and Council [eds.], SAS User's Guide, SAS Institute, Inc., Raleigh, North Carolina, 1979).

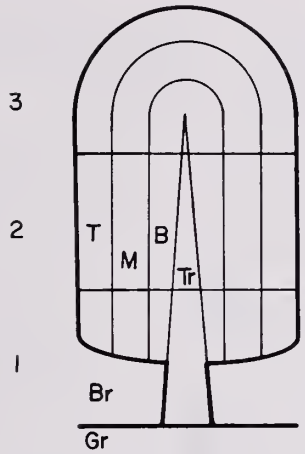

FIG. 1. Microhabitat categories. Gr = ground; Br = brush or understory; Tr = trunk; B, M, T = base, middle, and tips of branches, respectively. Trees were divided into three height classes.

Overlap in the use of microhabitats, foraging methods, and stances was calculated for each species pair using Pianka's (Proc. Natl. Acad. Sci. 71:2141–2145, 1974a) formula:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$

where p_{ij} and p_{ik} represent the proportional use of category i by species j and k, respectively. The mean proportion of foraging motions in each category was used as a measure of p_i.

TABLE 1

OCCURRENCE AND ABUNDANCE OF CORE SPECIES IN 30 MIXED FLOCKS

Species	N[a]	% in mixed flocks	No. flocks with species	Indiv./flock when in flocks	
				$\bar{x} \pm$ SD	Range
Black-capped Chickadee	113	97	29	3.8 ± 2.4	1–10
Chestnut-backed Chickadee	40	100	13	3.1 ± 1.6	1–6
Golden-crowned Kinglet	390	95	27	13.8 ± 8.5	1–35
Ruby-crowned Kinglet	48	85	26	1.6 ± 0.8	1–3
Downy Woodpecker	20	90	14	1.3 ± 0.5	1–2

[a] Total number of individuals observed.

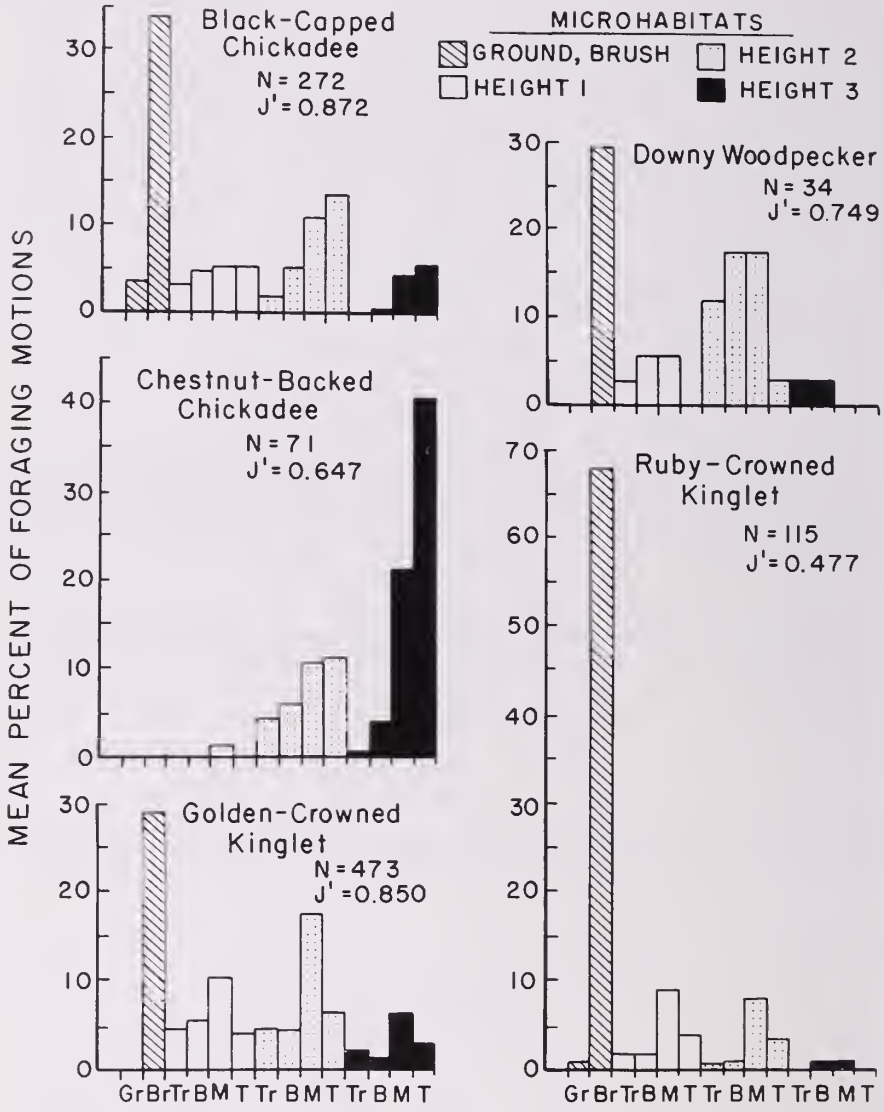

FIG. 2. Use of foraging microhabitats by core species. Abbreviations for microhabitats as in Fig. 1.

Overall overlap for species pairs was measured in two ways. Product overlap ($\Pi\ O_{jk}$), the product of overlap values for each dimension, is appropriate when complete independence of niche dimensions exists. Summation overlap ($\Sigma\ O_{jk}$), the arithmetic mean of overlap values, is appropriate when complete dependence of dimensions occurs. In reality, these

TABLE 2

RESULTS OF ANALYSES OF VARIANCE AND DUNCAN'S NEW MULTIPLE RANGE TESTS FOR BETWEEN-SPECIES (WITHIN-ROW) COMPARISONS OF MICROHABITAT USE

Microhabitat[a]	ANOVA *P*	Species differences[d]				
		BCC[c]	CBC	GCK	RCK	DW
Gr	0.0001	a	b	b	b	b
Br	0.0001	b	c	b	a	b
Tr 1	0.23	—	—	—	—	—
B 1	0.12	—	—	—	—	—
M 1	0.02	b	b	a	ab	ab
T 1	0.20	—	—	—	—	—
Tr 1	0.005	bc	bc	b	c	a
B 2	0.001	b	b	b	a	b
M 2[b]	0.03	—	—	—	—	—
T 2	0.002	a	ab	b	b	b
Tr 3[b]	0.03	—	—	—	—	—
B 3	0.32	—	—	—	—	—
M 3	0.0001	bc	a	b	c	c
T 3	0.0001	b	a	bc	c	bc

[a] Gr = ground, Br = branch, Tr = trunk, B = base of branch, M = middle of branch, T = tip of branch; numbers refer to height classes.

[b] No species differences were detected by Duncan's new multiple range test.

[c] Species common names abbreviated, see Table 1.

[d] Species with the same letter are not significantly different in their proportional use of a microhabitat.

two measures tend to underestimate and overestimate actual overlap, respectively, because neither complete independence nor dependence is likely (Cody, Competition and the Structure of Bird Communities, Princeton University Press, Princeton, Massachusetts, 1974; Pianka 1974a).

Niche breadth (foraging diversity) was estimated for each dimension using the formula $J' = H'/H'_{max}$ (Pielou, J. Theoret. Biol. 13:131–144, 1966) where $H' = \sum_{i}^{n} p_i \log p_i$, p_i is the proportion of observations in resource state *i*, and H'_{max} is the maximum possible diversity, i.e., when p_i's are equal. Small values of J' (approaching 0) indicate specialization; large values (approaching 1) indicate generalization.

Flock composition and size.—Mixed-flock size ranged from 3–108 individuals ($\bar{x}$ = 30.4, SD ± 24.8, N = 30). Number of individuals of core species in flocks ranged from 2–45 ($\bar{x}$ = 19.4, SD ± 11.2). Core species and their order of abundance in flocks were: Golden-crowned Kinglets (*Regulus satrapa*) > Black-capped Chickadees (*Parus atricapillus*) > Chestnut-backed Chickadees (*P. rufescens*) > Ruby-crowned Kinglets (*R. calendula*) > Downy Woodpeckers (*Picoides pubescens*). Dark-eyed Juncos (*Junco hyemalis*), Yellow-rumped Warblers (*Dendroica coronata*), Pine Siskins (*Carduelis pinus*), and Bushtits (*Psaltriparus minimus*) occasionally flocked with core species. Statistics describing the occurrence and abundance of core species in mixed flocks are presented in Table 1.

Niche relationships.—All core species foraged throughout the habitat (Fig. 2), but each differed to some degree in the proportional use of each microhabitat (Table 2). Feeding was concentrated in brush for all species except the Chestnut-backed Chickadee. As a result, microhabitat overlap was high (Table 3). Microhabitat niche breadth (J') was relatively large

TABLE 3
SPECIES-PAIR OVERLAP FOR MEASURED NICHE DIMENSIONS

Species[a] pair	Microhabitat	Method	Stance	Overall	
				ΠO_{jk}	ΣO_{jk}
BCC × GCK	0.951	0.996	0.958	0.907	0.968
BCC × RCK	0.908	0.993	0.812	0.732	0.904
BCC × DW	0.855	0.725	0.732	0.689	0.771
GCK × RCK	0.857	0.999	0.907	0.777	0.921
GCK × DW	0.899	0.713	0.657	0.421	0.756
RCK × DW	0.777	0.711	0.279	0.154	0.589
CBC × BCC	0.325	0.998	0.985	0.319	0.769
CBC × GCK	0.331	0.989	0.932	0.305	0.751
CBC × RCK	0.051	0.986	0.722	0.036	0.586
CBC × DW	0.197	0.706	0.841	0.117	0.581
$\bar{x}$	0.615	0.882	0.783	0.446	0.760
SD	±0.346	±0.145	±0.208	±0.309	±0.142

[a] Species common names abbreviated, see Table 1.

for all species except the Ruby-crowned Kinglet which foraged almost exclusively in brush (Fig. 2).

Gleaning was the most common foraging method used by all core species except the Downy Woodpecker. Accordingly, foraging method overlap was high (Table 3) and niche breadth (J') small (Fig. 3). Species usually foraged in an upright or hanging stance (Fig. 4). To a lesser extent, Golden-crowned and Ruby-crowned kinglets flew in pursuit of food; hovering (gleaning while flying) was more common than flycatching. Stance overlap was high for all species pairs, except Ruby-crowned Kinglets and Downy Woodpeckers; Downy Woodpeckers usually hung whereas Ruby-crowned Kinglets were usually upright when foraging (Table 3). J' for stance was high for all species except the Downy Woodpecker (Fig. 4).

Overall niche overlap was highest among Black-capped Chickadees, Golden-crowned Kinglets, and Ruby-crowned Kinglets (Table 3; mean species-pair $\Pi O_{jk} = 0.805$, mean species-pair $\Sigma O_{jk} = 0.931$); other species pairs exhibited little overall niche overlap.

Aggression.—All observed aggressive interactions (N = 79) were intraspecific and involved the following species (number of interactions in parentheses): Golden-crowned Kinglet (57), Black-capped Chickadee (10), Ruby-crowned Kinglet (7), and Chestnut-backed Chickadee (5).

Discussion.—The relationship between niche overlap and competition between species has been the subject of considerable controversy in the field of community ecology. Problems have arisen when measures of overlap have been erroneously equated with the competition coefficient of the Lotka-Volterra competition equation (Pianka 1974a). Substituting in this way, one would conclude that competition is greatest in communities where overlap is high. Alternatively, if resources are abundant relative to use, overlap between potential competitors could be great without the negative consequences of competition. Indeed, current theory predicts that maximum tolerable overlap should be greater where competition is reduced (niche overlap hypothesis [Pianka, Am. Nat. 106:581–588, 1972; Sale 1974; Schoener,

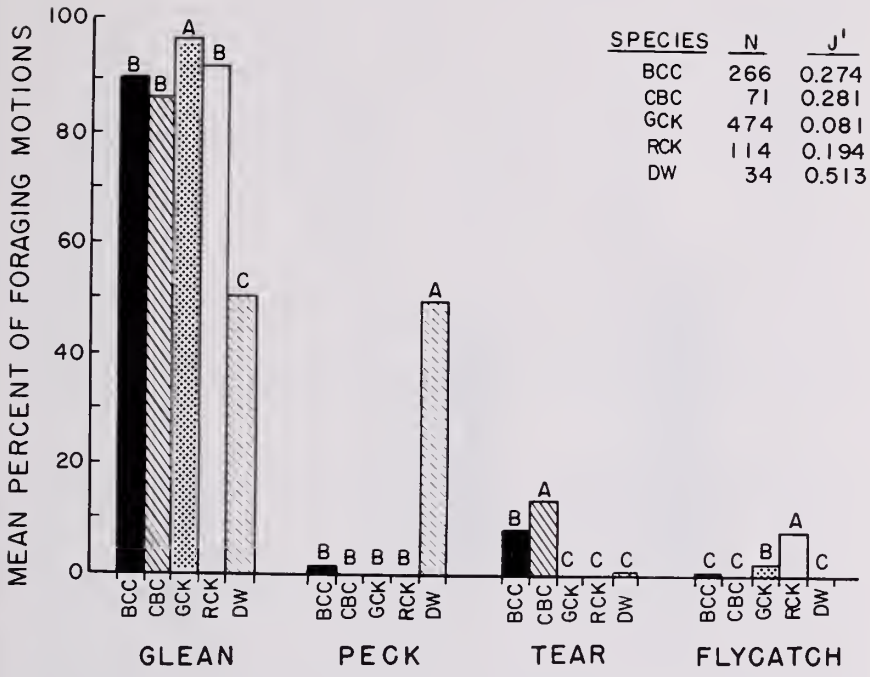

FIG. 3. Foraging methods used by core species. Abbreviations of species' common names given below bars. Means with the same letter (top of bars) are not significantly different (Duncan's new multiple range test, within-method comparisons only).

Science 185:27–39, 1974; Wiens and Rotenberry, Oecologia 42:253–292, 1979]). Data from a variety of locations and organisms seem to support the niche overlap hypothesis (Alerstam et al., Oikos 25:321–330, 1974; Pianka 1974a; Yeaton, Ecology 55:959–973, 1974; Diamond and Marshall, Emu 77:61–72, 1977; Rotenberry and Wiens, Ecology 61:1228–1250, 1980; Rosenberg et al., Auk 99:260–274, 1982; Schluter, Ecology 63:1504–1517, 1982).

For comparative purposes, we used data from Morse (1970, 1978) to calculate O_{jk} for wintering mixed flocks in deciduous woodland sites in England, Maryland, Louisiana, and Maine. Foraging microhabitat was the only niche dimension comparable among studies, but, this may be the most relevant dimension for niche differentiation in insectivorous, arboreal birds (MacArthur and MacArthur, Ecology 42:594–598, 1961; Pianka, Evolutionary Ecology, Harper and Row, New York, New York, 1974b). Additionally, morphological changes are not essential for many shifts in microhabitat usage, but are usually necessary for changes in foraging stance, foraging method, and diet (Yeaton 1974, Diamond and Marshall 1977). Thus, one might expect species to be able to adjust microhabitat use to the prevailing competitive milieu as documented in the bark-foraging guild of central Illinois (Williams and Batzli, Condor 81:122–132, 1979a; Wilson Bull. 91:400–411, 1979b). Indeed, Black-capped Chickadees, Golden-crowned and Ruby-crowned kinglets, and Downy Woodpeckers foraged in different microhabitats in different geographical regions. Brush was used

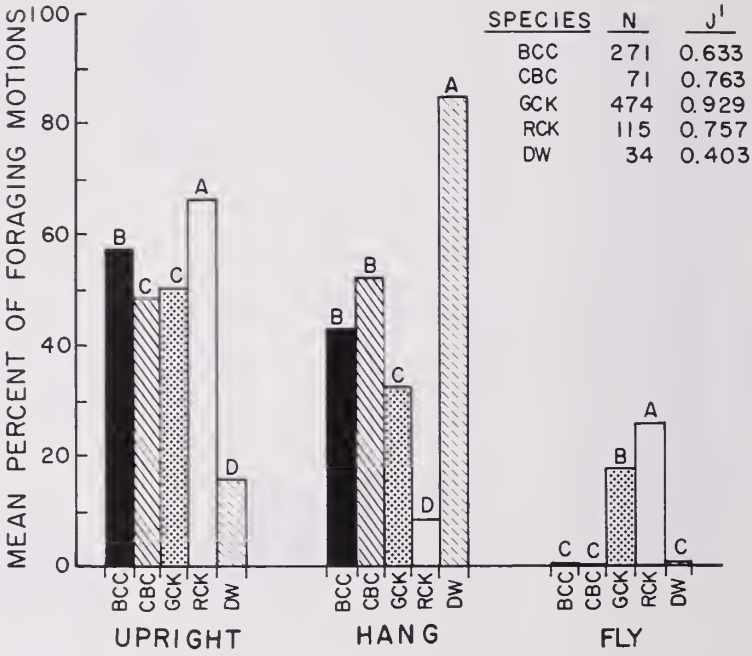

FIG. 4. Foraging stances used by core species. Abbreviations of species' common names given below bars. Means with the same letter (top of bars) are not significantly different (Duncan's new multiple range test, within-stance comparisons only).

heavily by all species in Washington, but this zone was little used in Morse's (1970, 1978) study areas except by Ruby-crowned Kinglets (an apparent brush specialist). In the east, Black-capped and Carolina chickadees foraged most on the middle section of branches; Golden-crowned Kinglets foraged most in low tips and brush; and Downy Woodpeckers foraged mainly on tree trunks (Morse 1970). Comparison of microhabitat overlap values among geographic regions, then, may be most illustrative of the relative importance of competition in light of the niche overlap hypothesis.

Mean species-pair overlap in microhabitat use (all core species considered) decreased geographically as follows: Washington (five species, $\bar{x} = 0.615$, SD $\pm$ 0.236), England (six species, $\bar{x} = 0.576$, SD $\pm$ 0.236), Maryland (seven species, $\bar{x} = 0.484$, SD $\pm$ 0.304), Louisiana (seven species, $\bar{x} = 0.466$, SD $\pm$ 0.287), and Maine (three species, $\bar{x} = 0.395$, SD $\pm$ 0.236), although this trend was not statistically significant (one-factor ANOVA, $F_{(4,65)} = 0.801$, $P > 0.50$). Overlap in microhabitat use for species pairs common to Washington and Morse's (1970) North American study areas did exhibit a significant geographical trend, in which species-pair overlap declined from Washington to Maine (Table 4).

Niche breadth should be greater under less intense competition and, therefore, should be positively correlated with niche overlap (Ulfstrand 1977, Wiens and Rotenberry 1979). Data from North American flocks suggest such a trend but are incomplete. Microhabitat J' for Black-capped Chickadees (and Carolina Chickadees) decreased from Washington (0.87),

TABLE 4

MICROHABITAT OVERLAP FOR SPECIES PAIRS COMMON TO SEVERAL STUDY AREAS[a]

Species pair[b]	Washington	Maryland[c]	Louisiana	Maine
BCC × GCK	0.951	0.830	0.618	0.544
BCC × RCK	0.908	—	0.602	—
BCC × DW	0.855	0.586	0.632	0.519
GCK × DW	0.899	0.391	0.299	0.123
RCK × DW	0.777	—	0.260	—

[a] Data for Maine, Maryland, and Louisiana were reanalyzed from Morse (1970).

[b] Significant location ($F_{(3,6)} = 10.132$, $P < 0.01$) and species-pair effects ($F_{(2,6)} = 7.285$, $P < 0.03$) were detected with two-factor ANOVA.

[c] Carolina Chickadees (*P. carolinensis*) were used in place of Black-capped Chickadees in overlap calculations for Maryland and Louisiana. Carolina Chickadees replace Black-capped Chickadees in east-central and southern states and the species are considered ecological equivalents (Brewer, Auk 80:9–47, 1963).

Maryland (0.74), Maine (0.70), and Louisiana (0.60); J' for Golden-crowned Kinglets decreased from Washington (0.85), Maryland (0.61), and Maine (0.59) (this study; Morse 1970).

The above evidence suggests that interspecific competition within western Washington mixed flocks in winter is low relative to other North American flocks. Two other pieces of information support this interpretation: large flock size (Washington mean >2 times mean flock sizes reported by Morse [1970, 1978]) and the absence of observed interspecific aggression in Washington (interspecific aggression was observed commonly in all flocks studied by Morse [1970, 1978]). A decline in the frequency of aggression might also occur in an intensely competitive environment where costs outweighed benefits. If this were the case, however, it would be surprising to observe intraspecific aggression as frequently as we did.

Why would the level of competition vary among these locations? Decreasing niche overlap values among regions are paralleled to some extent by decreasing mean winter temperature and presumably a concomitant decrease in arthropod availability. Louisiana is the exception to this climate/overlap trend because it has higher average winter temperatures than the other study locations but moderate overlap values.

Western Washington winters are typically wet and mild (mean temperature approximately 4.4°C). Flying insects were often observed during our study. Similar winter weather conditions occur in England (also with high niche overlap values [Morse 1978]), and continued growth and reproduction of arthropods were reported by Gibb (Ibis 102:163–208, 1960).

Alternative hypotheses can be proposed which could conceivably account for the observed trends in niche overlap. For example, the availability of microhabitats in different locations may affect competition and/or niche relationships. Thus, most species in Washington may concentrate feeding in brush and exhibit higher overlap because brush microhabitats were more plentiful than in other locations. However, we would not expect such species convergence in microhabitat use if food resources were limiting. The distribution of food among microhabitats could also affect foraging patterns. It is difficult to assess the importance of these environmental variables at present because data are not available for each site. At any rate, it is quite possible that more than one factor contributes to the observed niche relationships in mixed flocks.

Whereas our data are suggestive, longer term studies, preferably encompassing a variety of environmental conditions (climate, food abundance, etc.) should be conducted to increase

our understanding of the mechanics involved in niche relationships within mixed flocks. Changes in niche overlap, niche breadth, interspecific aggression, and flock size would be particularly illustrative, although niche relationships can be completely understood only when knowledge of resource abundance and dynamics is secure (Wiens and Rotenberry 1979).

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Sexual dimorphism and parental role switching in Gila Woodpeckers.—Since the seminal work of Selander (Condor 68:113–151, 1966) sexual dimorphism in woodpeckers has generally been considered to be a mechanism for the reduction of competition for food between mates. For a pair of monogamous birds to raise young successfully, they must not only provide food, but must also excavate new nest cavities, clean the nest of fecal material, guard the young, defend the food supply from other birds, and so on. These activities can represent conflicting demands. Using an optimality approach, for instance, Martindale (Behav. Ecol. Sociobiol. 10:85–89, 1982) showed that an individual cannot simultaneously maximize both nest defense and food delivery rate. Size dimorphism may be used to advantage in performing various tasks simultaneously if the pair coordinates their activities, dividing the labor so that each bird specializes in those behaviors for which its size makes it more efficient. In this note, we document the size dimorphism of Gila Woodpeckers (*Melanerpes uropygialis*) and demonstrate that mates coordinate their activities. We consider sexual differences not only in morphology, but also in foraging behaviors, the propensities to attack other birds, and to guard the young as opposed to feeding them. We also present evidence of facultative role switching between mates.

Methods.—Four hundred Gila Woodpeckers were mist-netted in Tucson, Pima Co., Arizona, during the winter months, November–April, from 1971–1979. Lamm banded each bird; its exposed culmen, wing and tail lengths, and weight were measured before it was released. All lengths were measured to the nearest 1.0 mm, and weights to the nearest 0.1 g.

Behaviors were observed by Martindale in Saguaro National Monument (Tucson Mountain Unit), 25 km W of Tucson, during the breeding seasons of 1978–1980. Twelve pairs of birds were observed for at least 20 h. When the woodpeckers foraged on a desert shrub (foothill paloverde [*Cercidium microphyllum*] or desert ironwood [*Olneya tesota*]), the size of the branch the bird was on was noted as small (tertiary branches with leaves, < 2 cm in diameter), medium (secondary branches between the main trunk and the leaf branches, roughly 2–10 cm in diameter), or large (main trunks, >10 cm in diameter). Records were kept of all aggressive interactions with other birds, distances from the nest of individual birds, and delivery rates of food items to the nestlings (trip/h).

For the morphological measurements, summary statistics ($\bar{x}$, SD), parametric (t) tests for the differences between the sexes, and product-moment correlation coefficients (r) among variables were calculated with the BMDP software package on a UNIVAC 1100/82 computer. Two-way contingency tables were used to test for differences between sexes in the categorical data, i.e., parts of shrubs used and species of birds attacked. For ease of interpretation, these tables are summarized here as proportions of observations in each category

TABLE 1

$\bar{x} \pm$ SD AND DEGREE OF SEXUAL DIMORPHISM IN SELECTED MORPHOLOGICAL CHARACTERS IN *MELANERPES UROPYGIALIS*

Character	Males (N = 200)	Females (N = 200)	t[a]	Percent dimorphism[b]
Culmen length (mm)	29.8 ± 1.2	25.5 ± 1.1	37.8	14.6
Wing length (mm)	132.3 ± 2.7	127.1 ± 2.8	19.1	3.9
Tail length (mm)	85.0 ± 3.8	81.4 ± 3.5	9.8	4.2
Weight (g)	73.0 ± 3.6	62.6 ± 3.8	28.2	14.2

[a] All differences in size are significant at $P < 0.001$.
[b] Percent dimorphism is the difference between sexes relative to the male size.

for each sex, but the accompanying χ^2 tests of independence (sex × substrate, sex × species attacked) are based on the number of observations in all cells of the table.

Size, foraging, and aggression.—Male Gila Woodpeckers were significantly larger than females for each of the four variables measured (Table 1). This species is strongly dimorphic, even for a melanerpine. Selander's (1966:114) graph indicated an average of about 9% (SE = 4.4%) dimorphism in culmen length for 38 species, so our observed value of 14.6% for *M. uropygialis* is well above the average, although not extreme. Selander (1966) indicated that gilas from Baja California (*M. u. brewsteri*) were apparently more dimorphic than mainland birds (*M. u. uropygialis*). This may be the case, but Selander's data indicate *brewsteri* to be about 16% dimorphic in culmen length, which is only slightly greater than our value for *uropygialis*.

Correlations among the morphological characters were rather low (Table 2). Although 7 of the 12 possible correlations were significantly positive, none was greater than 0.47, and most were less than 0.20. Relatively little of the total variance in these characters, then, can be explained by a "size factor" as has often been done in multivariate studies (Sneath and Sokal, Numerical Taxonomy, Freeman and Co., San Francisco, California, 1973). An individual bird may be heavier than others, but weight does not necessarily reflect size of beak or wings. Similarly, mated pairs vary in their degree of dimorphism, depending on the character being considered. On average, however, it is clear that males are about 14% heavier and have 14% longer bills than their mates.

As predicted in the hypothesis that dimorphism reduces resource overlap between mates, we found significant sexual differences in the use of desert shrubs by these woodpeckers (N = 134 observations of males foraging on shrubs and 167 observations of females [$\chi^2 = 39.2$, df = 2, $P < 0.001$]). Males used small branches on only 6% of their visits to shrubs, and used large branches and trunks on 60% of their visits. Females, however, divided their effort nearly equally over all parts of these plants, spending 34% of their visits on small branches and 33% on large ones. Martindale (Ecology 64:888–898, 1983) shows that females also spent more time searching for adult insects on plant surfaces rather than pecking for sub-surface larvae. This pattern of males using larger branches and pecking more, while females use smaller branches and glean more has been found in several species of dimorphic woodpeckers (see, e.g., Hogstad, Ibis 120:198–203, 1978, Wallace, Condor 76:238–248, 1974).

Male Gila Woodpeckers were also more aggressive than the females: the males attacked other birds at roughly twice the rate of the females. At the nest most intensively studied,

TABLE 2

CORRELATIONS (*r*) BETWEEN MORPHOLOGICAL CHARACTERS IN *M. UROPYGIALIS*[a]

	Culmen[b]	Wing	Tail	Weight
Culmen length (mm)	—	0.11	0.10	0.18**
Wing length (mm)	−0.14*	—	0.31**	0.47**
Tail length (mm)	0.09	0.46**	—	0.24**
Weight (g)	0.10	0.28**	0.19**	—

[a] Males (N = 200) are above the main diagonal, females (N = 200) below.
* $P < 0.05$, ** $P < 0.01$.

for example, the male averaged 8.7 attacks/h, while the female averaged 4.6 attacks/h but the hourly rates varied considerably, depending on the time of day, season, and density of other birds.

What is more, the sexes attacked different birds (Table 3). The significant difference arises from the fact that males attacked other Gila Woodpeckers much more frequently than did females (there is no significant sexual difference if Gila Woodpecker attacks are deleted from the table). The difference may again stem from the dimorphism in body size; the males can drive off other males, but the females cannot generally do so. Many of the attacks on other Gila Woodpeckers occurred in the vicinity of the nests, and can be interpreted as defense of the nest, the young, and perhaps of the female. Agonistic behavior directed toward Gilded Flickers (*Colaptes auratus chrysoides*), Ash-throated Flycatchers (*Myiarchus cinerascens*), and Ladder-backed Woodpeckers (*Picoides scalaris*) may reflect competition for nest-sites. Brenowitz (Auk 95:49–58, 1978) argued that virtually all interspecific aggression in Gila Woodpeckers was for nest-sites.

But we witnessed many attacks of another sort, directed toward open nesting species: Cactus Wrens (*Campylorhynchus brunneicappillus*), House Finches (*Carpodacus mexicanus*), Curve-billed Thrashers (*Toxostoma curvirostra*), and White-winged Doves (*Zenaida asiatica*). All these species feed on saguaro (*Cereus giganteus*) flowers and fruit, a primary source of food and water for desert birds in the nesting season (Hensley, Ecol. Monogr. 24: 185–207, 1954). At least 20% of all deliveries to Gila Woodpecker nestlings consisted of saguaro pollen or fruit (Martindale 1983), so some of the observed aggression may be in defense of this resource.

Role switching between mates.—As indicated above, male Gila Woodpeckers are consid-

TABLE 3

BIRDS ATTACKED BY GILA WOODPECKER BY SEX[a]

	Species attacked[b]								
Sex	GW	FL	CBT	CW	ATF	HF	WWD	UI other	No. obs.
Males	0.76	0.03	0.02	0.02	0.09	0.03	0.02	0.05	239
Females	0.49	0.04	0.07	0.04	0.15	0.09	0.05	0.06	130

[a] Proportions of attacks toward each species are indicated; $\chi^2 = 29.5$, df = 7, $P < 0.005$.
[b] GW = Gila Woodpecker, FL = Flicker, CBT = Curve-billed Thrasher, CW = Cactus Wren, ATF = Ash-throated Flycatcher, HF = House Finch, WWD = White-winged Dove, UI = Unidentified.

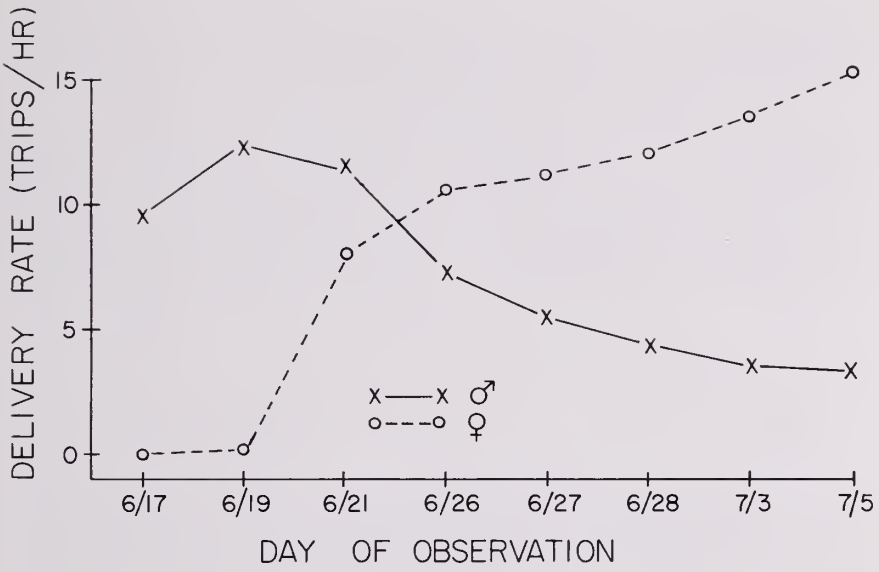

FIG. 1. Rates of food deliveries for a pair of mated Gila Woodpeckers on 8 mornings of observation in 1979.

erably larger than females, and are more aggressive, especially toward conspecifics. Males generally spent more time than females guarding the nest rather than foraging, and males, but not females, exhibited prolonged defensive behavior after experimental attacks (Martindale 1982). If the female stopped feeding the young, however, the male switched to foraging rather than defense. At one nest-site intensively studied in 1979, for instance, the female was exceptionally wary and made no deliveries during the first morning of observation, and only one the second morning. Instead, she stayed close to the nest (mean distance = 51 ± 50.8 m, N = 156 plant visits) repeatedly giving the low intensity alarm call. On the third day of observation the female began bringing food, and subsequently increased her rate each day. During this period, she went much farther from the nest than before (mean distance = 148 ± 96.9 m, N = 350 visits), as expected for increased foraging efficiency (Martindale 1982). Since the variances in distance from the nest were correlated with the means, we used log-transformed data for significance tests (see Sokal and Rohlf, Biometry, 2nd ed., Freeman and Co., San Francisco, California, 1981:419). The change in distance by the female after she resumed delivering was highly significant ($t = 14.7$, df = 504, $P < 0.001$).

As shown in Fig. 1, the male compensated for the changes in the female's rate by changing his own rate of feeding the young. When the female initially stopped delivering food, the male maintained a very high foraging rate and went farther from the nest (mean distance on 17 and 19 June: 126 ± 75.9 m, N = 200 visits). As the female increased her rate, however, the male decreased his rate, and stayed closer to the nest (mean distance after 26 June: 73 ± 63.9 m, N = 200 visits). Again, this change in distance was significant ($t = 219$, df = 398, $P < 0.01$). When not actively foraging and delivering, the birds guarded the nest.

The observed temporal pattern appears to represent role reversal by the sexes rather than

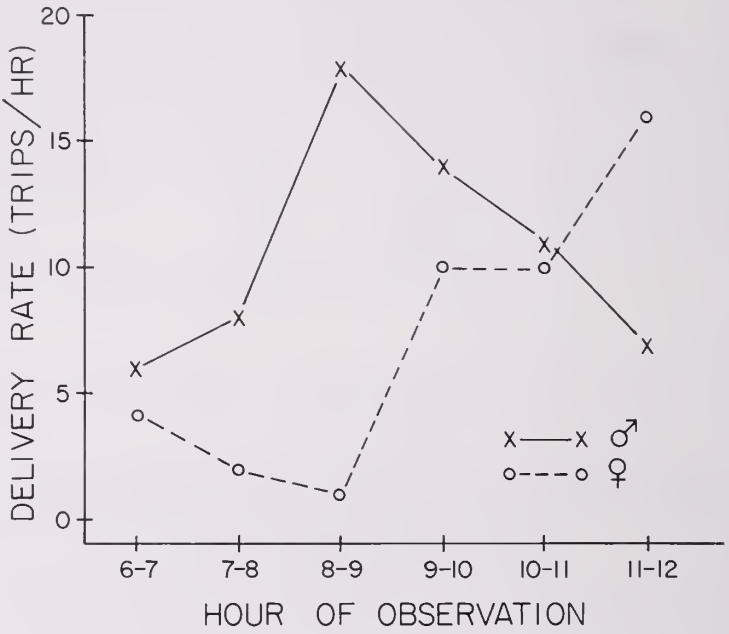

FIG. 2. Hourly rates of food deliveries, for the same pair of birds as in Fig. 1. Data are for 21 June 1979, the day the female resumed delivery.

seasonal differences in parental investment (in the sense of Andersson et al., Anim. Behav. 28:536–542, 1980). No similar trends were seen at the other nests where the females were unperturbed. Moreover, role switching often occurred over much shorter time scales than parental investment theory would predict. For example, delivery rate changes by the male at the perturbed site occurred within an hour of changes in the female rate on the day the female resumed bringing food (Fig. 2), but the survival probabilities for parents and offspring clearly do not change appreciably over such short periods. On average, males maintained a rate of about 8 trips/h and females a rate of about 12 trips/h from 07:00 until 12:00, so the pattern does not reflect a diurnal rhythm. We do not know if the male was responding to the female's activities per se or to the vocalizations of the nestlings.

Facultative short-term role switching occurred in a variety of situations. At one site, the pair was able to incubate a second clutch in a different nest while feeding nestlings, by trading back and forth between incubation and food delivery. At 11 of the 12 nests, only the males removed fecal sacs. But at a nest where the male was excavating a second cavity, the female performed this behavior. If a female was guarding a nest or fledgling when a serious attack occurred, she would give alarm calls until the male took over defense, then switch to feeding the young. After experimental attacks (Martindale 1982), the males guarded the nest for an hour or more, but were relieved every 20 min or so by the female. This was short-term role switching: after being relieved, the male would forage for about 5 min, make one delivery to the nest, then resume his guard while the female resumed bringing food to the young.

It is clear from these observations that during the breeding season, the behavior of a Gila Woodpecker depends to a large extent on what its mate is doing. So while the pronounced size dimorphism disposes the sexes generally to perform different parental functions, these roles are not exclusive; they can be traded back and forth between mates.

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Effect of litter on leaf-scratching in emberizines.—Many species of emberizines turn leaves and other litter by a two-footed scratching movement resembling hopping, in which the litter is thrown rearward under the bird (Hailman, Wilson Bull. 85:348–350, 1973). These scratches are performed sequentially in bouts, where the probability of adding another scratch to a bout is constant and hence independent of the number of scratches already performed in the bout (Hailman, Wilson Bull. 86:296–298, 1974). The quantitative model expressing this relationship predicts that the log frequency of bouts having s or more scratches ($\log f_s$) is a linear function of the number of scratches/bout (s):

$$\log f_s = (s - 1)\log p + \log B, \qquad (1)$$

where p is the constant probability of adding another scratch, $\log p$ is the slope and $\log B$ is the intercept of the linear regression. The present study evaluates one ecological variable previously suggested as possibly affecting the value of p: the amount of litter on the ground.

Equation (1) predicts quantitatively the behavior of several species: the White-throated Sparrow (*Zonotrichia albicollis*) and Dark-eyed Junco (*Junco hyemalis*) originally studied (Hailman 1974) and further considered in the present study, the White-crowned (*Z. leucophrys*) and Fox (*Passerella iliaca*) sparrows studied subsequently (Hailman, Wilson Bull. 88:354–356, 1976), and Rufous-sided Towhee (*Pipilo erythrophthalmus*) studied independently by E. H. Burtt, Jr., and me (Burtt and Hailman, Wilson Bull. 91:123–126, 1979). Furthermore, Burtt showed that p depends in part upon the amount of food available, in that towhees scratch in longer bouts as food becomes scarcer. I had suggested that p depends in part on the amount of litter (Hailman 1974), so it is possible that p is a compound variable, and the present experiments were set up to test the effect of litter.

The study plot consisted of a rectangle outside my study window in Madison, Dane Co., Wisconsin. The plot was divided in half, creating north and south meter-square quadrats. All litter was raked to the dividing line between the two quadrats, one measuring cup of about 235 cm^3 of mixed bird seed was scattered homogeneously over each area, and then all litter was raked over one of the two plots, thus creating a "littered" and a "bare" area. Wind, squirrels, and the birds themselves quickly scatter litter so that the bare area does not remain truly bare for long, nor does the littered area remain homogeneously littered; there is, however always a distinct difference in the amount of litter on the two sides.

I observed white-throats and juncos foraging the two areas for about 2 days, then reraked

and reseeded the plots, and switched sides by raking the litter onto the previously bare plot. The first littered plot was chosen at random, and then alternated with each reseeding. The study was conducted in autumn of 1973–76 and 1979, between the time that leaves had mostly fallen and the first snow covered the ground. The study is based on 1584 bouts containing a total of 2316 scratches observed during 39 observation periods on 25 different dates.

Statistical treatment of the data consists of least-squares regression of log f_s and s, with the goodness-of-fit to linear relationship expressed by the coefficient of determination (r^2). This statistic, which is the square of the correlation coefficient (r), more sensitively indicates the degree of fit than a simple test for the statistical significance of linearity, which is always highly significant in these data. The central tendency could be expressed by the mean number of scratches/bout, but a more sensitive measure is the probability (p) of adding another scratch—the antilog of the slope in equation (1). There is apparently no completely valid statistical technique for evaluating the difference between two regression lines of cumulative frequencies (indeed, past contributions in this series have attempted no such tests).

In ordinary linear regression, the slope-coefficient a (=log p) approaches a normal deviant whose variance (V) is the square of the slope's calculated standard error (equations found in most texts on parametric statistics), so I have evaluated a difference in slopes as

$$t = (a_1 - a_2)/(V_1/N_1 + V_2/N_2)^{1/2}, \quad (2)$$

where N is the number of points on the regression line for a data set. The number of degrees of freedom (df) is only approximately calculatable in such a t-test using unknown variances that cannot be assumed equal and the calculation itself is arduous, so I have used simply $df = N_1 + N_2 - 2$, which is strictly valid only when the variances are assumed equal. In all cases I have tested for equality of variances using Fisher's ratio (F = larger V/smaller V) and the variances could not be shown significantly different in any case where a t-test indicated a significant difference in slope. These methods are not strictly valid because f_s at a given s is not independent of f_s at some other value of s, so the reader may accept or ignore the outcome of t-tests as he pleases: it is a crooked wheel, but the only one in town.

The first concern was whether there is some systematic bias in the north and south plots. I recorded $B = 306$ bouts of scratching by white-throats in the north and 234 bouts in the south plot when littered, and the calculated probabilities of adding an additional scratch were found to be $p = 0.30$ and 0.23, respectively; the difference in slopes was not significant ($t = 1.354$, $df = 7$, $P_t = 0.22$, two-tailed). Similar data from the junco yielded $p = 0.31$ and 0.32 for 301 and 291 bouts, respectively, with an insignificant difference ($t = 0.203$, $df = 10$, $P_t = 0.84$, two-tailed). When the plots were bare for the white-throat, the values were $p = 0.14$ and 0.10 ($t = 1.30$, $df = 4$, $P_t = 0.26$, two-tailed) for 48 and 198 bouts, and for the junco were $p = 0.28$ and 0.09 for 122 and 76 bouts (sample too small for statistical test because V cannot be calculated in the latter regression). Therefore, no differences between the two plots could be established, and the data from the two were combined for testing between littered and bare areas.

Fig. 1 shows that, as predicted, a greater amount of litter causes White-throated Sparrows to scratch in longer bouts. The variances are not different ($F = 1.88$; $df = 2,4$; $P_F = 0.265$), but the difference in slopes is highly significant ($t = 5.16$, $df = 6$, $P_t = 0.0011$, one-tailed). Similar data for the Dark-eyed Junco (Fig. 2) show the same pattern, but the difference in slope is not nearly so great The F-ratio shows the variances to be significantly different ($F = 8.78$; $df = 4,5$; $P_F = 0.17$), so t-tests were run both with $df = N_1 + N_2 - 2$ and the more arduously calculated approximation of equation (2). In both cases the difference in slopes was not quite statistically significant ($t = 1.60$, P_t's = 0.072 and 0.085, one-tailed).

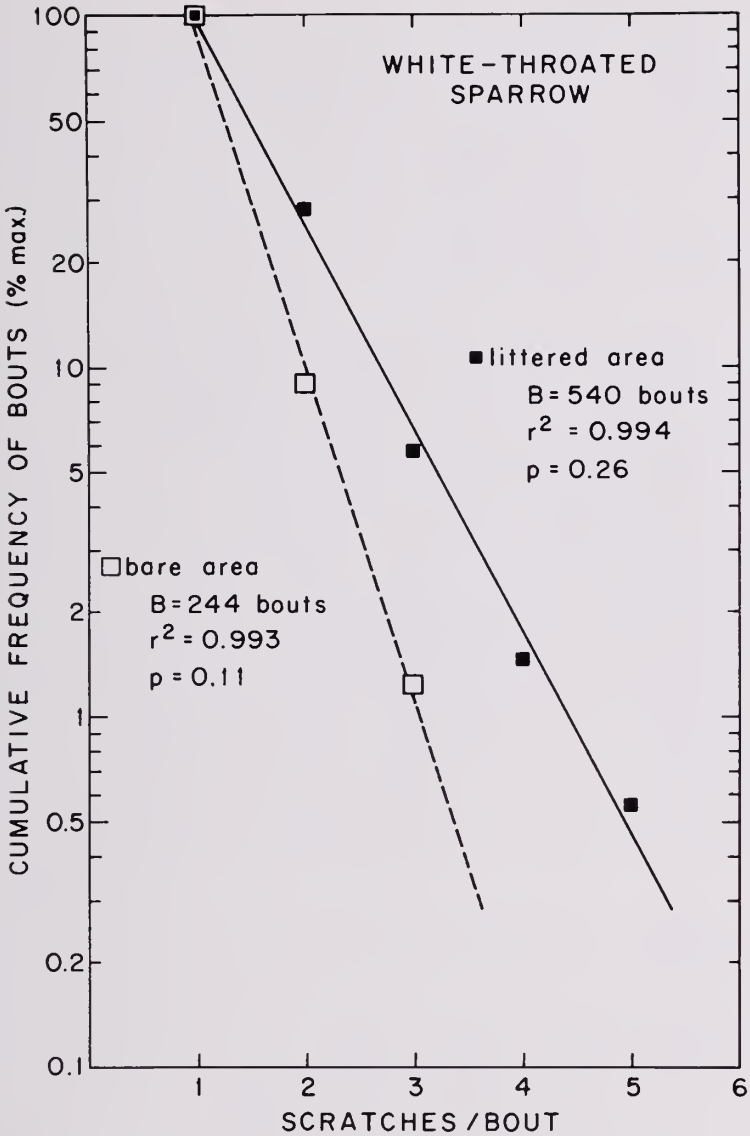

FIG. 1. Linear relationships between s (scratches/bout) and the frequency of bouts having s or more scratches plotted logarithmically ($\log f_s$) for the White-throated Sparrow. B is the number of bouts of scratching observed and r^2 the coefficient of determination expressing the fit to linearity. The lines drawn are fitted by least-squares regression. The difference in slopes between littered and bare areas is statistically significant (see text).

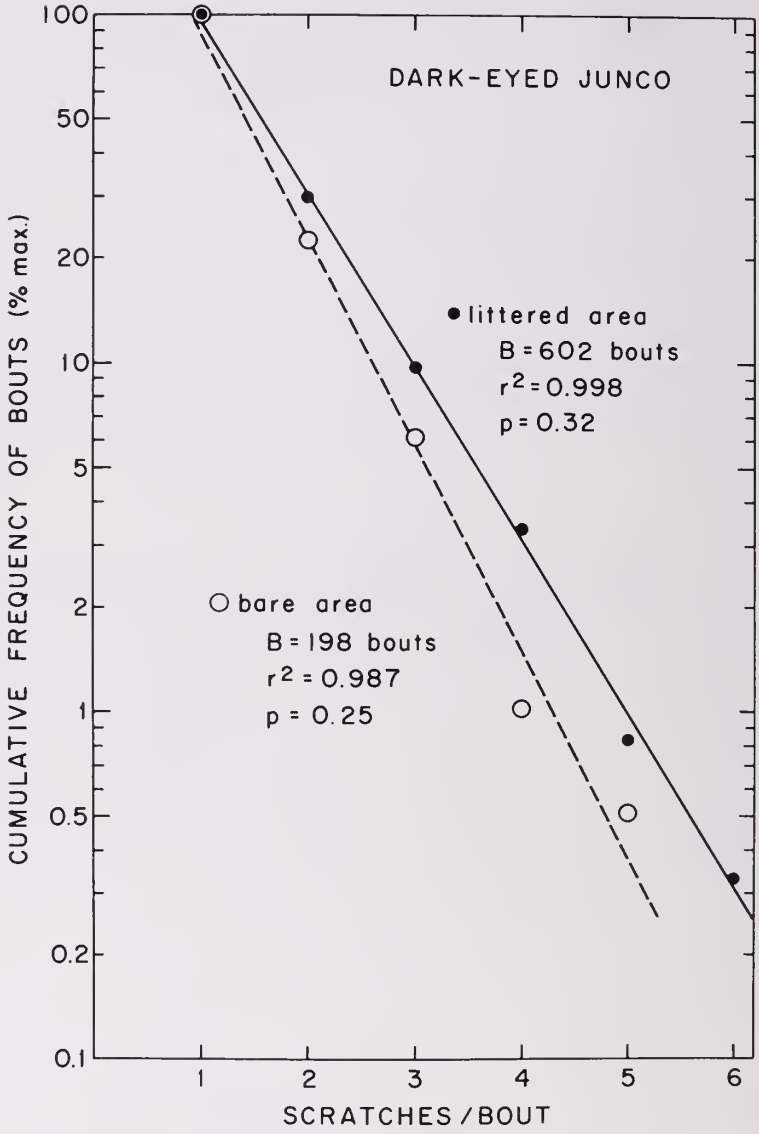

FIG. 2. Similar linear relationships in the Dark-eyed Junco (see Fig. 1). The difference in slopes is not quite statistically significant (see text). For evaluation of differences between the two species in a given area, see statistical comparisons given in the text.

Therefore, even though the difference is in the predicted direction of longer scratching bouts in the leaved area, the difference cannot unequivocally be established as real.

When I originally looked at these two species, I had the impression that white-throats scratched in longer bouts than did juncos, and this initial impression was consistent with slight differences in slopes of their data when later studied (Hailman 1974). However, I noted that the difference might be due to differences in scratching sites chosen by the two species, white-throats choosing more littered sites. The present data allow species comparisons within a particular site. In both sites it is the junco, not the white-throat, that has an absolutely higher probability of adding scratches to a bout (compare p-values of Figs. 1 and 2). In the littered site this difference is not significant ($t = 1.96$, $df = 9$, $P_t = 0.082$) but it can be established as real in the bare site ($t = 4.22$, $df = 6$, $P_t = 0.006$). It appears, then, that juncos rather than white-throats scratch in longer bouts under similar ecological conditions.

From the results in the figures, I conclude that the amount of litter is a variable affecting the length of scratching bouts. It should be pointed out that there was no control for food in these experiments, begun years before Burtt's experiments showing the importance of food in determining the length of bouts. At the beginning of each reseeded plot the amount of food was equal, but is seems likely that in the bare area seed became scarcer more rapidly than in the littered area, thus raising the value of p in the bare area and hence minimizing the differences in slope shown in the figures. Despite this mitigating effect, the present experiments established the reality of litter as another factor determining the probability of scratching. It is not possible on the basis of present evidence, however, to combine quantitatively the effects of litter and food on scratching; we can say only that both play a role in the quantitative determination of emberizine foraging. Nor do litter and food exhaust the possible variables affecting the probability of scratching; the hunger of the bird, for example, may also play a role, as may social factors such as companions scratching nearby.

The apparent contradiction between this and the previous study (Hailman 1974) with regard to species' differences is probably attributable to a number of factors. First, the difference found in the previous study is small and probably trivial. If real, it may have been due to observing white-throats more frequently in heavily leaved areas where the probability of scratching is relatively high, and juncos in less littered areas where the probability of scratching is lower. The present study was not constructed so as to measure preference for foraging site and any possible difference in site-preference cannot be resolved by data presently available.

Finally, it seems worth pointing out that these experiments serve to emphasize the importance of quantitative testing of intuitive hypotheses derived from anecdotal observations. The results in one case confirm the incidental observations that litter helps determine the length of scratching bouts, but in the other case reject the incidental observations that white-throats scratch in longer bouts than juncos. We thus come one step closer to understanding in detail the foraging behavior of a species and the nature of differences among species.

Acknowledgments.—I am grateful to J. R. Baylis and E. H. Burtt, Jr. for criticizing the manuscript draft, and to M. Gates and G. A. Clark, Jr. for their reviews.—Jack P. Hailman, *Dept. Zoology, Univ. Wisconsin, Madison, Wisconsin 53706.* *Accepted 14 September 1983.*

Wilson Bull., 96(1), 1984, pp. 126–128

Quantitative assessment of the nesting habitat of Wilson's Phalarope.—The nesting habitat of Wilson's Phalarope (*Phalaropus tricolor*) has been described as short grass or sedge meadows near sloughs and temporary or permanent lakes and ponds in the prairie regions of North America (Bent, U.S. Natl. Mus. Bull. 142, 1927; Hohn, Auk 84:220–244, 1967; Howe, Condor 77:24–33, 1977; Johnsgard, The Plovers, Sandpipers and Snipes of the World, Univ. Nebraska Press, Lincoln, Nebraska, 1981).

Methods.—I examined quantitatively the nest-site characteristics and apparent nesting habitat selection criteria of Wilson's Phalarope at Crescent Lake National Wildlife Refuge, Garden Co., Nebraska. Crescent Lake is located in the Nebraska Sandhills, an extensive area of stabilized sanddunes oriented at right-angles to prevailing westerly winds. Small lakes, marshes, and meadows are located in the interdune valleys. The vegetation surrounding lakes and in marshes consists predominantly of inland saltgrass (*Distichlis stricta*), Baltic rush (*Juncus balticus*), chair-maker's rush (*Scirpus americanus*), hardstem bulrush (*S. acutus*), clustered-field sedge (*Carex praegracilis*), spike rush (*Eleocharis macrostachya*), and common cattail (*Typha latifolia*). Bomberger (M.S. thesis, Univ. Nebraska, Lincoln, Nebraska, 1982) presented a more complete description of the area. The most common nesting associates of Wilson's Phalarope in these Sandhills areas were American Avocets (*Recurvirostra americana*), Willets (*Catoptrophorus semipalmatus*), Blue-winged Teal (*Anas discors*), Gadwall (*A. strepera*), Northern Shovelers (*A. clypeata*), American Coots (*Fulica americana*), Red-winged (*Agelaius phoeniceus*) and Yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds, and Marsh Wrens (*Cistothorus palustris*).

Observations were made during the breeding seasons of 1980 and 1981. Nests were located by systematically searching the meadows and marshes. All nests were marked and visited periodically to check their progress. As each nest was located, a 50-m transect was laid out parallel to the lake, with the nest being the center point. Since plant communities may change as distances from water change, all transects were laid out parallel to lakeshores with all points on each transect the same distance from water. Ten 1-m^2 sampling quadrats were randomly placed along each transect. In both 1980 and 1981, I measured average and maximum vegetation height, percent bare area, stem density, shoreline slope, distance to standing water, compass vector of the nest relative to the nearest lake, and the lake surface area. In addition in 1981, I measured percent grass cover, thickness of the litter mat, plant-stem diameter, above-ground biomass, and interstem distance.

For comparative purposes, in 1981, all variables were also measured for sites in the meadows and marshes where phalaropes were not found nesting and where their behavior did not indicate an interest in nesting. "Non-nesting" transects did not overlap any "nesting" transect. Non-nesting transects also were oriented so as to parallel lakeshores at the same distance from the water as the average nesting transect. An effort was made to select non-nesting transects as randomly as possible. They were sampled at approximately the same time in the season as were nest-sites.

Nesting and non-nesting habitat measurements were analyzed in the following ways. A Chi-square test was performed on the compass vector of the nest relative to the center of the nearest lake to determine if birds showed a preference for a particular side of the lake or a compass orientation. Shannon-Weaver species diversity indices (H') were calculated for the nesting and non-nesting habitat plant communities and compared with a *t*-test to determine if they were significantly different (Poole, An Introduction to Quantitative Ecology, McGraw-Hill, New York, New York, 1974). All multivariate analyses were performed using the SAS package (Helwig and Council, Statistical Analysis System [SAS] User's Guide,

TABLE 1

MEAN ± SE (RANGE), AND SIGNIFICANCE LEVELS OF NESTING AND NON-NESTING HABITAT CHARACTERISTICS

Character	Nesting		Non-nesting		
	1980	1981	1981	F	$P<$
Average veg. height (cm)	31.7 ± 1.8 (24.9–45.8)	25.6 ± 1.3 (15.5–36.3)	68.3 ± 4.0 (45.7–88.7)	105.78	0.001
Maximum veg. height (cm)	55.0 ± 2.9 (38.8–71.9)	45.7 ± 2.3 (30.2–64.9)	112.7 ± 5.2 (77.0–137.6)	135.74	0.001
Percent bare area (%)	22.5 ± 1.4 (12.5–31.1)	17.6 ± 2.0 (6.5–42.0)	31.7 ± 4.5 (6.0–59.0)	9.71	0.005
Percent grass cover (%)	—	99.9 ± 0.03 (99.6–100.0)	98.6 ± 0.7 (91.5–100.0)	4.27	0.05
Stem density (stems/m^2)	3876 ± 381 (1059–5900)	4385 ± 271 (1497–6410)	2935 ± 480 (665–7240)	4.54	0.05
Thickness of litter mat (cm)	—	0.74 ± 0.14 (0.0–2.7)	3.0 ± 0.4 (0.8–5.5)	33.68	0.001
Shoreline slope	0.21 ± 0.02 (0.10–0.34)	0.16 ± 0.02 (0.08–0.38)	0.32 ± 0.07 (0.06–0.96)	4.61	0.05
Distance to water (m)	4.6 ± 0.9 (1.8–11.5)	4.2 ± 0.8 (2.1–16.8)	—	1.84	0.2
Stem diameter (mm)	—	1.5 ± 0.04 (1.3–1.8)	5.1 ± 0.7 (1.7–7.9)	36.02	0.001
Above ground biomass (g/m^2)	—	829 ± 50.0 (548–1472)	1446 ± 172.0 (688–2812)	11.86	0.002
Interstem distance (cm)	—	1.7 ± 0.5 (0.9–2.3)	3.0 ± 0.5 (1.2–4.8)	20.25	0.001
Lake surface area (ha)	43.7 ± 39.6 (0.03–399.7)	32.2 ± 21.8 (0.03–399.7)	102 ± 36.5 (1.9–399.7)	1.73	NS

SAS Institute Inc., Cary, North Carolina, 1979, 1981) and the SPSS package (Nie et al., Statistical Package for the Social Sciences [SPSS], 2nd ed., McGraw-Hill, New York, New York, 1975). A multivariate analysis of variance (MANOVA) was performed on all of the habitat measurements to test for differences between nesting and non-nesting habitat in 1981 and between nest-site habitat in 1980 and 1981. Any overall differences found were tested with univariate F-tests to identify variables which were significantly different between habitat sites (Kleinbaum and Kupper, Applied Regression Analysis and other Multivariable Methods, Duxbury Press, North Scituate, Massachusetts, 1978).

Stepwise discriminant function analysis (SDFA), in two forms, was performed on the 1981 nesting and non-nesting habitat measurements to identify variables providing the best dis-

crimination between the two areas. In order to identify all of the variables which contributed significantly ($P < 0.05$) to the discrimination the backward-elimination procedure of stepwise DFA was performed. The forward-selection procedure of stepwise DFA was performed to identify the three variables which were the most critical ($P < 0.05$) to the discrimination.

Results and discussion.—Twelve nests in 1980 and 10 in 1981 were found and habitat associated with them was measured quantitatively. Twelve non-nesting areas were sampled in 1981. The compass vectors of the nest-sites relative to the nearest lake did not differ significantly from random in either 1980 ($\chi^2 = 0.22$, df = 7, NS) or 1981 ($\chi^2 = 0.57$, df = 7, NS). Nine of 19 plant species found in non-nesting areas also grew in the nesting areas. The species diversity indices (H') did not differ significantly ($t = 1.43$, df = 137, NS) between the nesting and non-nesting area plant communities. H' ± SE for nesting habitat was 2.31 ± 0.08 and for non-nesting habitat was 2.48 ± 0.095.

Means ± SE, ranges, and significant differences between the variables are presented in Table 1. The MANOVA showed a significant overall difference between the nesting and non-nesting areas ($F[18,7] = 67.56$, $P < 0.001$). Ten variables were significantly different between the two areas as shown by univariate F-tests. The MANOVA indicated no significant overall difference between the results for 1980 and 1981 ($F[8,20] = 1.61$, $P < 0.19$). Because Wilson's Phalaropes do not appear to return to the same site year after year (M. A. Howe, pers. comm.), this result is likely based primarily on selection of appropriate nesting vegetation.

Seven variables—maximum vegetation height, stem density, percent bare area, percent grass cover, above ground biomass, interstem distance, and average vegetation height—were shown to contribute significantly to the discrimination by the backward-elimination procedure of stepwise discriminant function analysis. All of these variables were also shown to be significantly different between nesting and non-nesting areas. Shoreline slope, stem diameter, and thickness of the litter mat, all significantly different between the two sampling areas, did not make significant contributions to the discrimination.

The three variables shown to provide the best discrimination between nesting and non-nesting areas by the forward-selection procedure of stepwise DFA are maximum vegetation height, percent grass cover, and average vegetation height. It can be seen in Table 1 that large differences in average and maximum vegetation heights existed between nesting and non-nesting areas. The means of both the average and maximum vegetation height were approximately 2.5 times greater in the non-nesting areas than in the nesting areas. However, the means of percent grass cover in the two areas differed by only 1.3%. The relative magnitude of these three differences imply that vegetation height is the major nesting habitat selection criterion for Wilson's Phalarope in Nebraska. Although these birds usually nest in meadows in the vicinity of a lake or pond, characteristics of the vegetation, especially vegetation height, are seemingly more important selection criteria than proximity of a nest-site to a body of water. This should be borne in mind when managing habitat for Wilson's Phalaropes.

Acknowledgments.—I thank C. R. Brown, A. Joern, and P. A. Johnsgard for their help during the course of this study and for reading and commenting on the manuscript. I also thank the U.S. Fish and Wildlife Service for allowing me access to Crescent Lake NWR, especially C. F. Zeillemaker, the manager. This study was supported by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History.—Mary L. Bomberger, *1939 Brower Rd., Lincoln, Nebraska 68502.* *Accepted 1 May 1983.*

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First confirmed nesting of a goshawk in Maryland.—On 24 June 1980, I discovered a nest of a Northern Goshawk (*Accipter gentilis*) in Garrett County, Maryland. The goshawks built the nest at a height of 8 m in the crotch formed by a main branch of a large red oak (*Quercus rubra*). Sticks and twigs from deciduous trees formed the nest foundation. The nest was lined with deciduous leaves and was sparsely decorated with a few small sprigs of white pine (*Pinus strobus*). Observation from a sapling near the nest tree revealed two downy white young estimated to be 1 week old. With the use of a telephoto lens, several photographs were made of the young in the nest.

The structure and situation of the nest-site were similar to the published accounts of goshawk nesting habitat in the eastern United States (Allen, Nesting ecology of the goshawk in the Adirondacks, M.S. thesis, State Univ. New York, Syracuse, New York, 1978). The nest was in a large (>4000 ha) contiguous woodland atop a plateau, 400 m from the edge of a 10–30° slope. The nest tree was approximately 300 m from a stream.

In Birds of Maryland and the District of Columbia, Stewart and Robbins (N. A. Fauna No. 62, USDI, Fish and Wildlife Service, 1958) mention only one nest record of goshawk for the State, "In 1901, a pair was present all summer and nested about 3 miles [4.8 km] above Jennings in Garrett County (Behr, Auk 31:548, 1914)." Behr's original article does not mention finding a nest and claims both adults "were shot by a native."

The goshawk's known breeding range has been expanding southward in recent years (Peterson, A Field Guide to the Birds, 4th ed., Houghton Mifflin Co., Boston, Massachusetts, 1980), with a nesting reported from as far south as Kentucky (J. Ruos, pers. comm.), and one recent nesting reported in West Virginia (G. Hall, pers. comm.). However, the present observation appears to be the first verified nesting of goshawk in Maryland.

Acknowledgments.—I am indebted to C. S. Robbins and M. R. Fuller of the USF&WS, Migratory Bird and Habitat Research Laboratory for assistance in preparing this note.—D. Daniel Boone, *Dept. Natural Resources, Maryland Natural Heritage Program, Annapolis, Maryland 21401.* *Accepted 2 Aug. 1983.*

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Pair separation in Canada Geese.—Canada Geese (*Branta canadensis*) are generally believed to remain paired with the same mate as long as both survive (Delacour, Waterfowl of the World, Vol. IV, Country Life, London, England, 1964). This note documents the separation of a pair of mated Canada Geese and subsequent formation of two new pairs. The observations were made in 1973–74 at the Crex Meadows Wildlife Management Area in northwestern Wisconsin. Many of the geese nesting in the vicinity were individually marked with neckbands (Zicus, J. Wildl. Manage. 45:830–841, 1981).

The observations concern one pair in which both members were neckbanded (pair A), a second pair in which only the female was neckbanded (pair B), and a neckbanded adult male of unknown breeding status (male C). All four adult marked geese were captured together and neckbanded while flightless on the marsh used for brood rearing and molting. Seven of eight goslings fledged by the two pairs were also neckbanded at the same time. Family members were identified by their mutual participation in greeting and triumph displays (Lorenz, On Aggression, Harcourt, Brace, and World, New York, New York, 1966; Raveling, Behaviour 37:291–319, 1970) and were observed together repeatedly throughout the summer and autumn in 1973.

In 1974, the first geese returned to a pasture-river staging area 5 km southeast of Crex Meadows on 9 March. Mated pair A returned with their four neckbanded 1973 offspring and were first observed on the morning of 11 March and were seen loafing together that evening. The next sighting of the family members was on 16 March at which time male A was accompanied by the four offspring. Female A was approximately 100 m away along the river bank with male C. Greeting displays between female A and male C suggested that the two had formed a new pair (AC).

Three of the neckbanded members from family B returned to the study area in 1974, but their arrival dates and behavior suggested the family was no longer intact. One yearling was first seen on 12 March while the female from pair B and another yearling offspring arrived at the staging area on 3 April. At this time, female B was unpaired and was never seen associating with either neckbanded 1973 offspring. By 5 April, male A and female B were observed engaging in greeting and triumph ceremonies that indicated they had paired. The 1973 offspring from pair A remained with male A from 16 March until about 10 April when new pair AB began establishing a nesting territory, at which time the offspring were evicted from the family.

Pair AC initiated a nest on 11 April and all six eggs hatched. Likewise, pair AB initiated a nest on 14 April and all seven eggs hatched. Both pairs fledged young in 1974.

The formation of new pairs in Canada Geese after the death of one member has been documented by several authors (Kossack, Am. Midl. Nat. 43:627–649, 1950; Sherwood, Trans. N. Am. Wildl. Nat. Resour. Conf. 32:340–355, 1967; Jones and Obbard, Auk 87: 370–371, 1970). In contrast, new pairings in Canada Geese while both pair members are alive have seldom been described. MacInnes et al. (J. Wildl. Manage. 38:686–707, 1974) mention pair separation for Canada Geese nesting at the McConnell River, Northwest Territories, but the circumstances were not documented. The reasons for the separation and re-pairing are unknown and puzzling since pair A successfully raised a brood in 1973 and the family returned to the breeding area together in 1974. The fact that the pair separated before the pair bond was reinforced by active territorial defense may be significant. In addition, geese that formed new pairs in 1974 shared the same molting area in 1973 and thus were probably familiar with each other. Mate swapping in other species generally believed to pair for life has been described for Sandhill Cranes (*Grus canadensis*) (Littlefield, J. Field Ornithol. 52:244–245, 1981) and postulated as a rare but possible occurrence for Snow Geese (*Anser caerulescens*) (Cooke and Sulzbach, J. Wildl. Manage. 42:271–280, 1978).

Acknowledgments.—I thank the Wisconsin Department of Natural Resources, University of Minnesota, Daytons Natural History Fund, the Malvin and Josephine Herz Foundation and many other individuals for support and help with my Crex Meadows studies. S. Maxson offered useful suggestions on a draft of this note.—Michael C. Zicus, *Dept. Entomology, Fisheries, and Wildlife, Univ. Minnesota, St. Paul, Minnesota 55108.* (Present address: *Minnesota Dept. Natural Resources, Wetland Wildlife Research Group, 102 23rd St., Bemidji, Minnesota 56601.*) *Accepted 22 Aug. 1983.*

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Food habits of wintering Brandt's Cormorants.—Only two studies have examined the diet of Brandt's Cormorants (*Phalacrocorax penicillatus*) during winter. Baltz and Morejohn (Auk 94:526–543, 1977) described the food of six Brandt's Cormorants collected offshore in Monterey Bay, California; Ainley et al. (Condor 83:120–131, 1981) summarized results of an unpublished study on 13 specimens from near Vancouver Island, British Columbia

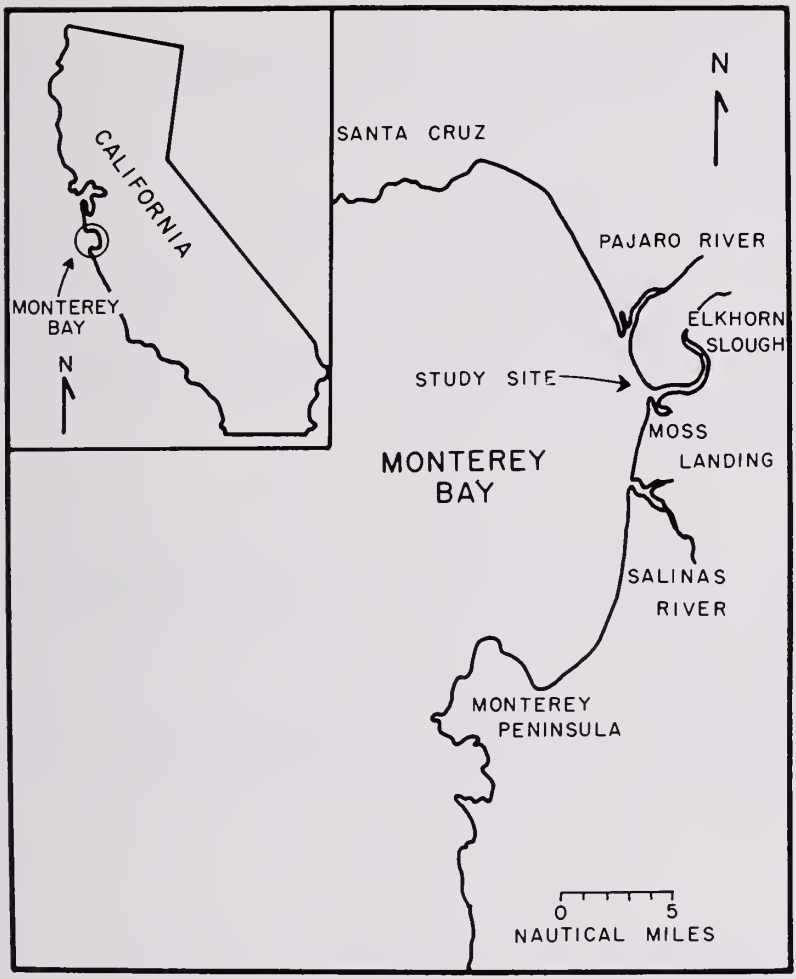

FIG. 1. Map of Monterey Bay, California, showing study area.

(this study also summarized all available information on the species' diet during summer). The present paper examines the food habits of Brandt's Cormorants feeding inshore in Monterey Bay during winter.

Eleven Brandt's Cormorants (9 male, 2 female) were collected from 1 December 1970–March 1971 inshore near Moss Landing, California (Fig. 1). Water depth varied from 25–50 m and the substrate was of sand and mud.

Cormorants were collected in the morning just after they had fed and contents of their esophagus, proventriculus, and ventriculus were removed. Food items consisted of either whole, undigested prey, referred to hereafter as whole prey samples, or fish otoliths. The

number of each species of whole prey was recorded and the volume of each item was determined by water displacement. Because otoliths represented prey captured by cormorants on previous feeding trips (probably on the day before the bird was obtained), they were treated separately and are referred to as otolith samples. Otoliths were washed and stored dry, and later identified with the aid of a reference collection. The number of fish represented in each otolith sample was determined by dividing the total number of otoliths (sagittae) by two.

The Index of Relative Importance (IRI) was used to rank the importance of each prey species in whole prey food samples. The IRI (number + volume) × (frequency) of each food item was established as a linear combination of its numerical importance, volumetric importance, and frequency of occurrence (Pinkas et al., Calif. Dept. Fish and Game, Fish Bull. 152:1–105, 1971). The value of the IRI ranges from 0, when all three values are 0, to 20,000 when all three indices are 100%. A modified Index of Relative Importance (mIRI) was used to rank the importance of each prey species in otolith food samples. It was also used to make comparisons with whole prey samples. The mIRI (number × frequency) ranges from 0, when both values are 0, to 10,000 when both indices are 100%.

The Brillouin formula:

$$H = (1/N)\left(\ln N! - \sum_{i=1}^{s} \ln N_i!\right)$$

where N is the total number of individuals and N_i is the number of individuals of the ith species, was used to calculate trophic diversity indices for prey items in stomach contents (Pielou, J. Theoret. Biol. 13:131–144, 1966; Am. Nat. 100:463–465, 1966). Trophic diversity was calculated for each food sample; the total accumulated trophic diversity of all food samples was calculated by randomly pooling individual samples (Hurtubia, Ecology 54: 885–890, 1973).

I used the index of Morisita (Mem. Fac. Sci. Kyusha Univ. Ser. E (Biol.) 3:65–80, 1959), as modified by Horn (Am. Nat. 100:419–424, 1966), to determine the degree of similarity of whole food and otolith samples. The coefficient of overlap was estimated by

$$C = \frac{2\sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2}$$

where s is the total number of food categories and the data are expressed as the numerical proportions x_i and y_i of prey items in the whole prey and otolith samples of i prey species in samples x and y. The coefficient varies from 0 when samples are completely distinct to 1 when samples are identical.

Brandt's Cormorants fed entirely on fishes (Table 1). Bottom dwelling species, principally Pacific sanddabs (*Citharichthys sordidus*), but also English sole (*Parophrys vetulus*), and plainfin midshipman (*Porichthys notatus*) were the most important prey items in both whole prey and otolith food samples. Juvenile rockfish (*Sebastes* spp.) were also important prey items. Though known to occur from bottom to mid-depths, they too were likely caught near the bottom judging from the preponderance of bottom species in the diet. These species are also important to Brandt's Cormorants in central California during summer, though their ranking may differ (Ainley et al. 1981).

The whole prey and otolith samples were quite similar ($C = 0.84$); the only apparent difference was that juvenile rockfish were more important in otolith samples. However, the difference was not significant (paired $t = 0.07$, $df = 9$, NS), which indicated that the cor-

TABLE 1

ANALYSIS OF 11 WHOLE PREY AND 10 OTOLITH SAMPLES FROM BRANDT'S CORMORANTS COLLECTED NEAR MOSS LANDING, CALIFORNIA

Prey species	Whole prey					Otolith		
	%N[a]	%V[b]	%FO[c]	IRI	mIRI	%N	%FO	mIRI
Scomberesocidae								
Cololabis saira	4.2	0.7	9.1	45	38	2.0	10.0	20
Scorpaenidae								
Sebastes spp. (juvenile)	4.2	2.5	9.1	61	38	38.0	30.0	1140
Atherinidae								
Atherinopsis californiensis	4.2	25.1	9.1	266	38	2.0	10.0	20
Bothidae								
Citharichthys sordidus	75.0	60.6	63.6	8624	4770	54.0	70.0	3780
Pleuronectidae								
Parophrys vetulus	8.3	5.4	18.2	249	151	2.0	10.0	20
Batrachoididae								
Porichthys notatus	4.2	5.7	9.1	90	38	2.0	10.0	20

[a] Percentage of total number of individuals.
[b] Percentage of total volume of individuals.
[c] Frequency of occurrence (%).

morants sampled probably fed consistently one day to the next in the study area, or in similar habitat with comparable fish populations.

The prey of Brandt's Cormorants feeding in the inshore zone in 1970–71 differed from prey of cormorants feeding offshore in 1974–75. Baltz and Morejohn (1977) found that midwater species, mostly juvenile rockfish, northern anchovy (*Engraulis mordax*), and market squid (*Loligo opalescens*) were the most important prey of wintering Brandt's Cormorants feeding in the offshore zone. None of these prey, except juvenile rockfish, was present in the diets examined during my study. However, the comparison is not conclusive because both studies were conducted over a short duration, 4 years apart, and the diet may well differ one year to another even in the same locality.

Individual trophic diversity indices averaged 0.0992 (range 0–0.3465) and 0.1692 (range 0–0.5868) for whole prey and otolith food samples, respectively, and were not significantly different (paired $t = 0.84$, df = 10, NS). The total accumulated trophic diversity was 0.7373 for whole prey, 0.8916 for otolith, and 0.9762 for all food samples combined. This latter value is 39% lower than the accumulated trophic diversity value reported by Baltz and Morejohn (1977). Whether prey available to Brandt's Cormorants are less diverse inshore than offshore in Monterey Bay needs further study.

The plot of the accumulated trophic diversity indices of Brandt's Cormorants (Fig. 2) appeared to approach an asymptote as the contents of individual samples were pooled. Hurtubia (1973) pointed out that if pooled samples reach the asymptote, food specialization and niche breadth of populations can be compared. If this is so, my results represent a good estimate of the food niche breadth of Brandt's Cormorants feeding inshore over a sand and mud substrate in Monterey Bay during the winter of 1970–71.

The relative importance of the study-site or similar habitat in Monterey Bay as feeding

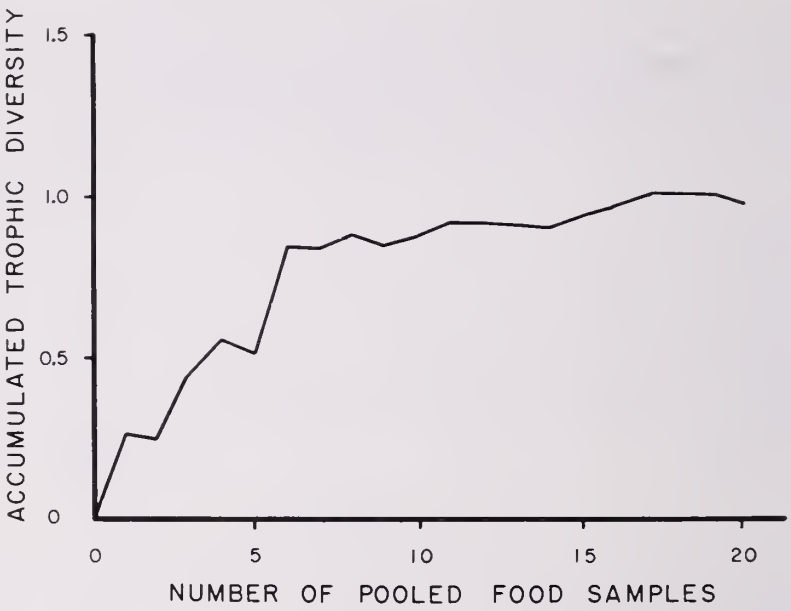

FIG. 2. Curve of accumulated trophic diversity vs counts of individual food samples of Brandt's Cormorants collected near Moss Landing, California.

areas of Brandt's Cormorants is unknown. No study has examined habitat use patterns of individual Brandt's Cormorants and little is known about feeding-site fidelity of individuals. My results, however, suggest that most of the cormorants collected had fed for at least 2 days on fish species predominantly found over a sand and mud substrate. Nevertheless, use of the study area by feeding adult Brandt's Cormorants was almost totally restricted to winter, although a few subadult birds used the study area throughout the year (Talent, unpubl.).

Apparently, most cormorants that fed at the study-site roosted on the numerous offshore rocks and islands around the Monterey Peninsula (Talent, unpubl.). The round trip from roosting site to the study area off Moss Landing was about 55 km. The energetic cost of these winter feeding flights is unknown, but cormorants making the trip were able to utilize an abundant food source, e.g., Pacific sanddabs, and avoid competition with the hundreds of Brandt's and Pelagic (*Phalacrocorax pelagicus*) cormorants that fed within the rocky inshore zone around Monterey Peninsula.

Acknowledgments.—I thank Joel Cohen and Carline Talent for assistance in collecting cormorants, and O. E. Maughan for critically reviewing the manuscript.—LARRY G. TALENT, *Moss Landing Marine Laboratories, Moss Landing, California 95039.* (Present address: *Dept. Zoology, Oklahoma State Univ., Stillwater, Oklahoma 74078.*) *Accepted 1 May 1983.*

Wilson Bull., 96(1), 1984, pp. 135–136

Opportunistic feeding by White-tailed Hawks at prescribed burns.—Attraction of certain hawk species to fire and smoke is a recognized phenomenon (Baker, J. Mammal. 21:223, 1940; Stevenson and Meitzen, Wilson Bull. 58:198–205, 1946; Komarek, Proc. Ann. Tall Timbers Fire Ecol. Conf. 9:161–207, 1969). The interpretation is that raptors feed opportunistically upon the prey chased from cover by fire passage (Baker 1940) or left without cover by the burn (Lawrence, Ecology 47:278–291, 1966; Beck and Vogl, J. Mammal. 53: 336–346, 1972).

White-tailed Hawks (*Buteo albicaudatus*) have been reported to congregate at prairie fires on the Texas coast. Stevenson and Meitzen (1946) described two 60-ha gulf cordgrass (*Spartina spartinae*) burns at Aransas National Wildlife Refuge (ANWR) which attracted 28 White-tailed Hawks. The hawks dived through the smoke to capture cotton rats (*Sigmodon hispidus*), pocket mice (*Perognathus* sp.), and grasshoppers (Acrididae). I report herein additional instances of White-tailed Hawks being attracted to fires.

During the afternoon of 14 January 1981, two adjacent 2-ha prescribed burns were conducted on a bunchgrass-annual forb community (Drawe et al., Welder Wildl. Contrib. No. 5, Ser. B, 1978) at the Welder Wildlife Refuge (WWR), 80 km NE of Corpus Christi, Texas. These two sites were separated by less than 1 km. Dominant species included seacoast bluestem (*Schizachyryium scoparium*), thin paspalum (*Paspalum setaceum*), and *Croton* spp. A White-tailed Hawk arrived within 5 min after initiation of the backfire and hovered in the smoke column. This behavior continued for the duration of the fire or approximately 20 min. About 10 min after the burn had been completed, this hawk flew to the ground and apparently captured prey.

On 15 January 1981, two adjacent 2-ha burns were initiated at 10:00 at WWR in a mesquite-mixed grass community (Drawe et al. 1978). Dominant plant species on this site included mesquite (*Prosopis glandulosa*), Texas wintergrass (*Stipa leucotricha*), and meadow dropseed (*Sporobolus asper*). Five White-tailed Hawks were attracted to and flew through the smoke. These hawks hunted from aerial vantage points by hovering and gliding and from mesquite trees. This hunting continued for the duration of the burn or about 30–45 min. Prey were captured but I was unable to identify the species.

Approximately 1 h after the end of this fire and 3 km away, a slower, more extensive burn attracted six additional White-tailed Hawks, one of which was in juvenal plumage. This burn was 35 ha but patchy in character. Numerous long-horned grasshoppers (Tettigoniidae) were flying ahead of the fire-front and in the rising smoke. The hawks grasped these grasshoppers in the air with their talons and fed while soaring. Occasionally, a hawk would glide to the ground, capture a grasshopper, and return to the air to consume the prey. This hunting continued for the duration of the fire, 2–3 h. White-tailed Hawks remained perched in trees and shrubs near these burns for nearly a week.

A 40-ha prescribed burn in gulf cordgrass occurred on 2 February 1981 at ANWR. This location is about 32 km NE of the WWR burns. Although it took nearly 1.5 h to complete the backfire, the headfire lasted about 10 min and the total procedure ended by 13:30. This burn attracted 14 White-tailed Hawks. They hovered near the ground and grasped prey in the ash. This feeding behavior continued throughout the afternoon. Other raptors soaring in and near the smoke column and hunting the burn included two Northern Harriers (*Circus cyaneus*), a Black-shouldered Kite (*Elanus leucurus*), an American Kestrel (*Falco sparverius*), and a Short-eared Owl (*Asio flammeus*).

No special effort was made to monitor the raptor populations at the WWR. However,

strip transects for birds were censused six times both before and after the cordgrass burns at the ANWR. The burn site and an adjacent control were surveyed and White-tailed Hawks were not recorded during any transect count. The hawks at the fire came from outside the immediate area of the burn.

In contrast to the WWR burns, the hawks at ANWR were not seen on subsequent days. Instead, numerous Turkey Vultures (*Cathartes aura*) and Caracaras (*Caracara cheriway*) fed on small carrion in the Aransas postburn site for at least 5 days. The Aransas headfire was a rapid conflagration and probably killed many cotton rats and snakes (Tewes, M.S. thesis, Texas A&M Univ., College Station, Texas, 1982). A fast, destructive burn leaving few possible prey could explain the failure of hawks to remain on this postburn.

Finally, on 22 February 1981, four more 2-ha Welder burns were conducted near the previously mentioned locations (two adjacent burns separated by 4 km from the other two adjacent burns); all failed to attract White-tailed Hawks. I have no explanation for this observation.

Although hawks may feed on rodents during and immediately following a fire, this may be only a short-lived advantage. An extensive and complete burn removes much of the vegetative cover and subsequently is poor habitat for most rodent species (Tewes 1982). This situation continues until regrowth provides adequate cover for small mammal re-establishment.

Acknowledgments.—Thanks is extended to L. Drawe, K. Butts, and especially S. Labuda for their assistance with my research. I am grateful to B. Thompson and D. Slack for providing comments on the manuscript. Also, Dr. J. Teer and the Welder Wildlife Foundation provided support for my study via the Edward H. and Winnie H. Smith Fellowship. This is Welder Wildlife Contribution No. 275.—Michael E. Tewes, *Rob and Bessie Welder Wildlife Foundation, P.O. Drawer 1400, Sinton, Texas 78387.* (Present address: *Caesar Kleberg Wildlife Research Inst., Box 218, Texas A&I Univ., Kingsville, Texas 78363.*) *Accepted 31 July 1983.*

Wilson Bull., 96(1), 1984, pp. 136–137

Swallows foraging on the ground.—Wolinski (Wilson Bull. 92:121–122, 1980) and Sealy (Wilson Bull. 94:368–369, 1982) reported Rough-winged Swallows (*Stelgidopteryx ruficollis*) obtaining food by landing on the ground. Both examples involved beaches, the swallows in one case apparently taking fly larvae from dead fish and in the other dead midges washed up on the beach. Although Sealy (1982) had not seen such actions by other swallows, Bent (U.S. Natl. Mus. Bull. No. 179, 1942 [Dover reprint, 1963]) included references to ground foraging by Tree Swallows (*Tachycineta bicolor*) and Purple Martins (*Progne subis*). Tree Swallows were reported picking up seeds from the ice of a frozen pond on 19 March 1939 and landing on a marshy shore apparently to feed on minute insects, and wintering swallows had taken crustacea that could hardly have been obtained on the wing (Bent 1942). In this note I report two more instances of apparent ground foraging by swallows, and integrate these with previous information to explain possible benefits of such unusual behavior.

On 28 May 1971, at Lac Hébécourt, Abitibi Co., Québec (48°31'N, 79°24'W), I watched about 15 Tree Swallows apparently foraging among decaying vegetation at the strand line on the lakeshore. The birds were hopping around, pecking at the debris, perhaps picking up fly larvae or other invertebrates, during 5 min that I watched from my cabin 30 m away. Their activity was focussed on the vegetation rather than on the much more extensive gravel areas of the beach, which suggested that they were obtaining food rather than grit. I did not approach them to identify possible food organisms, as I did not want to disturb birds which

might be stressed by lack of more typical food; the weather had been damp, with freezing temperatures at night, and insects were apparently scarce, as suggested by unusual behavior by other insectivorous birds (e.g., warblers sitting still probing into spruce cones, pers. obs.).

On 5 July 1975, and again the following day, I saw a Violet-green Swallow (*Tachycineta thalassina*) circling over and landing on patches of bare ground at the edge of a trailer park near Smithers, British Columbia (54°49′N, 127°11′W). While on the ground, the bird hopped around pecking at the substrate, looking all around between pecks. Two other Violet-green Swallows swooped low over the first bird on 6 July, and one of them also landed but was not seen to pick up anything. I inspected the ground where the swallow had been pecking; the only animals seen were several small spiders. Many other, more open locations nearby would have provided better opportunities for securing grit; Royama's (J. Anim. Ecol. 39: 619–668, 1970) observation that Great Tits (*Parus major*) regularly fed spiders to their young during the first week suggested that spiders may provide some important nutritional factor and thus be especially sought out.

Both Wolinski (1980) and Sealy (1982) attributed ground-foraging by Rough-winged Swallows to opportunistic use of a temporarily available, high-density food source, but neither the availability nor the density were obviously favorable in the other situations. Tyler's (*in* Bent 1942) observation of Tree Swallows picking up seeds from a frozen pond and mine of the same species foraging on a lakeshore, both occurred in early spring when flying insects were not readily available. This may have been true also of Wolinski's (1980) observation (on 22 May 1977), but Sealy (1982) explicitly noted flying insects nearby at the time of his sighting (31 May 1979). The other sightings quoted by Bent (1942) lack dates. Thus, ground-foraging may occur when aerial insects are scarce and grounded food is an easier food source.

Species which spend more of the year in cooler climates, whether by arriving early or remaining late in the breeding areas, or by wintering farther north, may be expected to benefit most by adapting to unusual food sources. The Tree and Violet-green swallows return earlier in spring than our other swallows, and these are also the only ones which winter regularly north of the Mexico-U.S. border, although Rough-winged Swallows do so to some extent. Observations of foraging by swallows in early spring or cold seasons would probably provide more records of ground-foraging, which may be more general than has been recognized.—Anthony J. Erskine, *Canadian Wildlife Service, P.O. Box 1590, Sackville, New Brunswick E0A 3C0, Canada.* *Accepted 7 June 1983.*

Wilson Bull., 96(1), 1984, pp. 137–138

Use of an interspecific communal roost by wintering Ferruginous Hawks.—Although much is known about the breeding biology of the Ferruginous Hawk (*Buteo regalis*), little is known about its habits during winter. The few individuals wintering in Utah's desert shrub habitats appear to be territorial and avoid the more gregarious Rough-legged Hawks (*B. lagopus*) and Bald Eagles (*Haliaeetus leucocephalus*) (Smith and Murphy, Sociobiology 3:79–98, 1978). This paper provides the first documentation of communal roosting by Ferruginous Hawks and also the first evidence that Ferruginous Hawks share roosts with other raptors.

Ferruginous Hawks were observed in Charles Mix County, South Dakota (43°04′N, 98°32′W), near the northeastern limit of the wintering range (A.O.U., Check-list Committee, Check-list of North American Birds, 5th ed., Lord Baltimore Press, Baltimore, Maryland, 1957). Roosting activity was recorded in the winter of 1975–76 during 25 early morning visits to a tree stand near Lake Andes. Between one and six Ferruginous Hawks used the roosting stand on 11 occasions, and between one and 33 Bald Eagles used it on 19. Hawks

used the roost from 2 December–13 February, and eagles used it from 29 December–15 March. On the nine mornings that the roost was used by both species, between one and three hawks and five and 28 eagles were present. No interspecific aggression was noted in the roost, and distances between hawks and eagles appeared similar to distances between conspecifics. Hawks left the roost 57–15 min before sunrise ($\bar{x} = 30$, SD ± 15), approximately the same time eagles departed. Hawks also tended to leave in the same direction as most departing eagles. The 0.6-ha roost consisted of 77 mature cottonwoods (*Populus deltoides*) that grew between Lake Andes and a cultivated field. Roost trees had a mean diameter of 51 cm (SD ± 20 cm) and an estimated median height of 18 m.

It is unlikely that a shortage of suitable roosting sites forced communal roosting because similar stands within 1 km of the roost were not used by individuals of either species. Ward and Zahavi (Ibis 115:517–534, 1973) proposed that communal roosting facilitates food-finding, and several workers have suggested that this explanation is applicable to Bald Eagles (Steenhof M.S. thesis, Univ. Missouri, Columbia, Missouri, 1976; Knight, M.S. thesis, Western Washington Univ., Bellingham, Washington, 1981; Stalmaster, Ph.D. thesis, Utah State Univ., Logan, Utah, 1981). Both Ferruginous Hawks and Bald Eagles were commonly seen during the day near concentrations of feeding waterfowl in agricultural fields near Lake Andes. Individuals of one or both species may have learned of these potential food sources from interactions at the roost.

Acknowledgments.—This note is a contribution from the Gaylord Memorial Laboratory (University of Missouri–Columbia and Missouri Department of Conservation cooperating). Support was provided by the Lake Andes National Wildlife Refuge, the National Wildlife Federation, the Office of Biological Services, U.S. Fish and Wildlife Service, and the Omaha District, U.S. Army Corps of Engineers. I wish to thank L. H. Fredrickson and S. S. Berlinger for advice and guidance throughout the study. L. S. Young provided helpful suggestions on the draft manuscript.—KAREN STEENHOF, *Gaylord Memorial Laboratory, School of Forestry, Fisheries, and Wildlife, Univ. Missouri–Columbia, Puxico, Missouri 63960.* (Present address: *Snake River Birds of Prey Research Project, Bureau of Land Management, 3948 Development Avenue, Boise, Idaho 83705.*) *Accepted 7 June 1983.*

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Serum chemical levels in captive female House Sparrows.—Until recently, there were relatively few studies which were conducted to specifically characterize the chemical constituents of the blood of birds. Even the well-established blood chemical levels of the domestic chicken (*Gallus gallus*) are mostly a result of the compilation of the data from a wide variety of other blood-related physiological investigations (Sturkie, Avian Physiology, Cornell Univ. Press, Ithaca, New York, 1954:32; Avian Physiology, 3rd ed., Springer-Verlag, New York, 1976:246; Van Tienhoven, Reproductive Physiology of Vertebrates, 3rd ed., Cornell Univ. Press, Ithaca, New York, 1983:180). Earlier, hematological investigations of nondomestic birds consisted of measurements of erythrocyte numbers and blood hemoglobin levels (Nice et al., Wilson Bull. 47:120–125, 1935), while later, blood protein levels also were determined (Dabrowski, Acta Biol. Cracoviensio, Ser. Zool. 9:259–275, 1966; Balasch et al., Poultry Sci. 52:1531–1534, 1973). More recently, the levels of carbohydrates, lipids, and serum enzyme activities have been among some of the other hematological values examined in wild and captive birds (Kern and de Graw, Condor 80:230–234, 1978; de Graw et al., J. Comp. Physiol. 129B:151–162, 1979; Driver, J. Wildl. Dis. 17:413–421, 1981; Gee et al., J. Wildl. Manage. 45:463–483, 1981; Franson, J. Wildl. Dis. 18:481–485, 1982;

TABLE 1
SERUM COMPONENTS AND ENZYME ACTIVITY LEVELS IN FEMALE HOUSE SPARROWS

Serum component (units)	No. of birds	Range	Mean ± SEM
Total protein (g/100 ml)	7	3.1–5.9	3.90 ± 0.23
Albumin (g/100 ml)	7	0.9–1.5	1.12 ± 0.08
Globulin (g/100 ml)	7	2.1–4.6	2.77 ± 0.33
Albumin/globulin ratio	7	0.3–0.6	0.44 ± 0.04
Calcium (mg/100 ml)	8	7.4–12.4	8.44 ± 0.72
Cholesterol (mg/100 ml)	6	197–228	211.00 ± 4.62
Glucose (mg/100 ml)	8	458–613	528.60 ± 22.36
Blood urea (mg/100 ml)	8	2.3–4.4	2.79 ± 0.25
Uric acid (mg/100 ml)	7	10.3–29.0	19.87 ± 2.27
Bilirubin (mg/100 ml)	7	0.6–2.2	1.13 ± 0.23
Alkaline phosphatase (U/L)	6	76–222	155.33 ± 20.16
Creatine phosphokinase (U/L)	8	356–6041	3357.1 ± 878.6
Lactate dehydrogenase (U/L)	8	1429–3947	2924.8 ± 285.6
Serum glutamate-oxalacetate transaminase (U/L)	8	112–1293	608.0 ± 137.8

Rehder et al., J. Wildl. Dis. 18:105–109, 1982). Similar data also were recently obtained in several common pet avian species (Rosskopf et al., Vet. Med./Small Anim. Clin. 77:1233–1239, 1982). The most comprehensive of these recent studies was that by Gee et al. (1981) who compared the hematological differences in 12 evolutionarily primitive species of captive cranes, geese, raptors, and quail. The modicum of similar comparative data in more recently evolved birds prompted the present investigation of the blood chemistry of the House Sparrow (*Passer domesticus*), as a representative of the evolutionarily most recent Passeriformes.

Serum constituents were measured in eight female House Sparrows by an Abbott VP Bichromatic Analyzer. The serum samples were obtained from four adults on 24 November and 4 December 1981. The birds, which were trapped locally, were caged for 2–4 weeks before sacrifice, during which time they were kept under natural photoperiods in an enclosed room at about 10–15°C, and provided with chick starter mash (approx. 16% protein) and water, ad lib. All birds were ether-anesthetized and blood samples obtained via cardiac puncture at about 17:00. The samples were transferred to clotting tubes, and upon clotting at room temperature, were centrifuged at 2800 rpm for 5 min. The collected serum was recentrifuged at the same speed and time, and frozen for assay the following morning. The assay procedure involved placing approx. 300–500 μl of serum into a sample cup in the analyzer. An onboard-computer controlled the batch-operated assay of the serum components. In a few instances, insufficient serum volume prevented the assay of some of the components (Table 1).

The level of serum total proteins in the House Sparrow (Table 1) is within about 20% of the levels reported in all other reproductively quiescent, captive or free-living birds (Dabrowski 1966, Balasch et al. 1973, Driver 1981, Gee et al. 1981, Rosskopf et al. 1982). The House Sparrow's serum albumin (A), globulin (G), and the A/G ratio (Table 1), however,

are similar only to those reported in free-living corvids (Dabrowski 1966). The 27–163% lower A/G ratios in the sparrow than the more primitive Gruiformes, Anseriformes, Falconiformes, and Galliformes (Driver 1981, Gee et al. 1981) is due to marked differences in either, or both, A and G. Serum calcium levels (Table 1) are similar to those of nonbreeding hens (Sturkie 1976:322) and pigeons (*Columba livia*) (Welty, The Life of Birds, 3rd ed., Saunders Co., New York, New York, 1982:165), and within 25% of those of captive, primitive birds (Gee et al. 1981), pet birds (Rosskopf et al. 1982) and wintering free-living and winter-captive White-crowned Sparrows (*Zonotrichia leucophrys*) (Kern and de Graw 1978).

Serum total cholesterol levels in the sparrows (Table 1) ranged from about 15% higher than in Falconiformes to 50% higher than in Gruiformes (Gee et al. 1981). Although cholesterol also was 50% higher than in captive White-crowned Sparrows, it should be noted that the cholesterol levels reported for the White-crowned Sparrows were for free-cholesterol, which is often about 25–50% less than the total blood cholesterol levels (Kern and de Graw 1978, de Graw et al. 1979, Kern, pers. comm.). The sparrow's cholesterol levels, however, were near the same levels found in the Hawaiian Goose (*Nesochen sandvicensis*) (Gee et al. 1981), cockerels (Van Tienhoven 1983:180) and hypercholesteremic strains of atherosclerotic pigeons (Wartman and Connor, J. Lab. Clin. Med. 82:793–808, 1973; Subbiah and Siekert, Br. J. Nutr. 41:1–6, 1979).

The House Sparrow was found to be markedly hyperglycemic (Table 1) when compared to most other birds (Sturkie 1976:211; Whitehead et al., Br. J. Nutr. 40:221–234, 1978; Gee et al. 1981). Whether these twice-normal glucose levels are characteristic of passerines, or caused by hormonal imbalances, or other stresses associated with captivity, is not known. That the sparrow's blood glucose concentration is only 18–32% greater than the upper normal ranges reported for pet Canaries (*Serinus canaria*), Cockatiels (*Nymphicus hollandicus*), and Budgerigars (*Melopsittacus undulatus*) (Rosskopf et al. 1982), suggests that high blood glucose levels may be typical of small, captive granivorous birds. Alternatively, the hyperglycemia may have resulted from gluconeogenesis from the high-protein diet the sparrows were fed, since it is known that small passerines only require about 8% protein diets for maintenance in captivity (Martin, pp. 365–379 *in* Proceedings of the General Meeting of the Working Group on Granivorous Birds, IBP, PT Section, S. C. Kendeigh and J. Pinowski, eds., Warsaw, Poland, 1972; Parrish and Martin, Condor 79:24–30, 1977). This possibility is further supported by the twice-normal uric acid levels in the House Sparrow (Table 1) than other birds (Driver 1981, Gee et al. 1981, Rosskopf et al. 1982). Similar increases in uric acid levels have been reported in chickens fed higher than normal protein diets (Featherson, Poultry Sci. 48:646–652, 1969). The presence of normal blood urea concentrations (Table 1) was to be expected as high-protein diets did not affect blood urea levels in chickens (Bell et al., Biochem. J. 71:355–364, 1959).

Bilirubin values in the House Sparrows (Table 1), surprisingly, were 2- to 9-fold greater than those found in the evolutionarily more primitive birds examined by Gee et al. (1981). That bilirubin values were near the normal ranges reported in human serum (Abbott Laboratories, Diagnostics Division, A-Gent Bilirubin, South Pasadena, California, 1980) probably is due to the higher erythrocyte numbers typical of small passerine birds, such as House Sparrows (Nice et al. 1935; Sturkie 1976:58; Chilgren and de Graw, Auk 94:169–171, 1977), than most other birds (Balasch et al. 1973, Sturkie 1976:58, Gee et al. 1981).

The relatively high serum enzyme activities of alkaline phosphatase in the sparrows (Table 1) were near those determined in fall-captive Sandhill Cranes (*Grus canadensis*) (Gee et al. 1981), American Black Ducks (*Anas rubripes*) (Franson 1982), and Mallards (*A. platyrhynchos*) (Driver 1981). Serum glutamate-oxalacetate transaminase (SGOT) activities were near the exceptionally high enzyme levels reported in Northern Bobwhites (*Colinus virgin-*

ianus) (Gee et al. 1981). In contrast, serum creatine phosphokinase (CPK) enzyme activities in the sparrows were 1.5 times those of fall-captive Mallards (Driver 1981), while lactate dehydrogenase (LDH) levels were about 3 times the highest values found in captive bobwhites, Peregrine Falcons (*Falco peregrinus*) (Gee et al. 1981), and Greater Indian Hill Mynas (*Gracula religiosa*) (Rosskopf et al. 1982). The exceptionally high SGOT and LDH enzyme levels in the sparrow may be attributed to drastic physiological changes which occurred when the birds were sacrificed since death-associated elevations of these enzymes have been previously reported in Mallards (Driver 1981). Elevations in LDH also have been reported to be caused by hemolysis (Rosskopf et al. 1982), although there was little evidence of hemolysis in the serum samples of the sparrows in this study. The markedly high CPK levels in the sparrows may have resulted from muscular damage during confinement and handling, since Driver (1981) found increases in CPK activities in captive and bait-trapped Mallards.

Although the results from avian blood analyses, especially serum enzymes, are difficult to compare when obtained from different laboratories (Gee et al. 1981), the values obtained in the sparrows in the present study are likely comparable with those reported by Driver (1981), Gee et al. (1981), Franson (1982), and Rosskopf et al. (1982). This is because the present results, as well as the results of those workers, were obtained by employing similar standardized autoanalyzer techniques. At the same time, there are a multitude of other factors, such as physical and environmental conditions, handling and sampling techniques, circadian and circannual rhythms, as well as sex, age, diet, and state of health of the birds, which could greatly affect the comparability of the data among these studies.

In spite of these and other limitations, it is apparent that the serum protein components, calcium, glucose, urea, and total cholesterol levels in House Sparrows are approximately near those previously reported in other more recently evolved passerine birds. Whether the exceptionally high bilirubin and uric acid levels present in the House Sparrow are typical of other passerines requires further study. It is probable that the elevated serum enzyme levels in the House Sparrow may not be typical and resulted from either disease or stresses associated with handling, sacrificing, and captivity of the birds. If our results also are representative of noncaptive House Sparrows, then they also imply that the levels of serum components previously reported in fowl, and other more primitive birds, are not necessarily typical of those found in the more recently evolved small passerine birds.

Acknowledgments.—We are grateful to the Newman Memorial County Hospital Laboratory for the use of their Abbott Analyzer. We thank Mrs. D. Schrader for running the assays. We also thank Dr. G. F. Shields for help in reviewing an earlier draft of this manuscript. This research was partially funded by a grant to JP from the Emporia State University Faculty Research Committee.—John W. Parrish and Michelle L. Mote, *Div. Biological Sciences, Emporia State Univ., Emporia, Kansas 66801.* *Accepted 15 June 1983.*

Wilson Bull., 96(1), 1984, pp. 141–142

Comments on Blancher and Robertson's "double-brooded Eastern Kingbird."—A note by Blancher and Robertson (Wilson Bull. 94:212–213, 1982) entitled "A double-brooded Eastern Kingbird," has prompted me to comment on its inculsion in a recognized, refereed journal. The authors describe a case of a supposed double brood in a pair of Eastern Kingbirds (*Tyrannus tyrannus*) (a species not known to be double-brooded), without presenting conclusive proof of the event. A pair of Eastern Kingbirds raised a brood of young, one (banded) of which fledged successfully, and then later a female was found incubating three eggs in a

nest 3 m distant from the other nest. The authors, by calculating time intervals and presumably by the proximity of the two nests, concluded that the same female was responsible.

Regardless of probability such a conclusion should only be based on incontrovertible proof (through marking) that the female in each case was the same bird. Several possibilities for error present themselves: the sexes are not separable in the field (except by behavior) and the female in question was apparently unbanded. A change in the title to "A possible double-brooded Eastern Kingbird" would have clarified the situation.—GEORGE K. PECK, *Dept. Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada. Accepted 25 Aug. 1983.*

Wilson Bull., 96(1), 1984, p. 142

Response to Peck.—The comment by Peck on our note "A double-brooded Eastern Kingbird" brings up a valid point. Since the female involved was not banded, we cannot be absolutely sure that the same female was responsible for both nests. Therefore, the title change he suggests might have been appropriate. However, we disagree with other statements in his comment.

He states that we based our conclusion that the same female was involved on the time interval between nests and the proximity of the two nests. He fails to mention that a banded fledgling from the first nest was present with the adults at the second nest, and that the two adults were seen with the fledgling during the four checks of the nest area between fledging of the first nest and discovery of the second nest. These observations strengthen our conclusion. He also states that "Several possibilities for error present themselves" yet he only refers to one valid possibility (unbanded female). The fact that the sexes are separable in the field only by behavior is irrelevant to the conclusion that the same female was involved in both nests.—PETER J. BLANCHER AND RALEIGH J. ROBERTSON, *Dept. Biology, Queen's Univ., Kingston, Ontario K7L 3N6, Canada. Accepted 21 Sept. 1983.*

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ORNITHOLOGICAL LITERATURE

ESTIMATING NUMBERS OF TERRESTRIAL BIRDS. By C. J. Ralph and J. M. Scott (eds.). Studies in Avian Biology No. 6, Cooper Ornithological Society, Allen Press Inc., P.O. Box 368, Lawrence, Kansas 66044, 1981:630 pp., numerous numbered text figs., tables, 8 appendices, literature cited, Readers Guide. $20.00.—Although an impossible task, this book comes very close to summarizing all of the major techniques for counting birds, along with their strengths and weaknesses, although more attention is paid to the latter. Besides the Introduction and Summary of the Symposium sections, the presented papers are divided into nine major topics: Estimating Relative Abundance (14 papers), Estimating Birds Per Unit Area (7 papers), Comparison of Methods (8 papers), Species Variability (4 papers), Environmental Influences (11 papers), Observer Variability (10 papers), Sampling Design (10 papers), Data Analysis (8 papers), and Overview (10 papers). Most of these sections have introductory and summary remarks by well known authorities in the field. Besides the presented papers there were also 36 poster papers, unfortunately listed by title only in the back of the proceedings. For a North American symposium, this had a decided International flair, with many of the presented papers by scientists from throughout the world.

The first major section, "Estimating Relative Abundance," mostly covers the Christmas Bird Count (CBC) and Breeding Bird Survey (BBS). Although both methods have strengths and weaknesses the latter seems to have a better "quality control" program and the data should be viewed as slightly more reliable than the former. Notwithstanding all of the problems associated with CBC data, Bock and Root do present some interesting uses of the data, especially for long term studies of wide geographical population shifts. It is certain that the BBS survey data are being under utilized by researchers and approaches to their use such as presented by Geissler and Noon should be encouraged. In Dawson's paper we are advised to census birds ". . . between 0930 and 1530 to avoid the rapid change in birds' conspicuousness near dusk and dawn." By so doing, a major component of the variance will be reduced. I might add that if you count when there aren't any birds out, naturally the variance will be low. Robbins presents information about the use of Winter Bird Population data in the concluding paper in Part I of this section.

Part II of this section is a hodge-podge of most of the remaining relative abundance estimators including: mist netting; playback techniques; playback/mapping; migration counts; atlasing; and Bull's indirect estimate paper covering nest counts, roost counts, fecal counts, track counts, feeding sites, dusting sites, and auditory cues. In his excellent summary of this section Rao compares statistical difference and biological difference. Being as guilty or more so as most in this regard, I am in the process of repenting and will no longer be content to say "significantly different at $P < 0.05$" and leave it at that.

The next major section covers "Estimating Birds Per Unit Area," better known as density. Despite the variety and elegance of methods presented in this section David Trauger's statement on p. 5 still obtains, "Bird censuses, that is total counts of birds in a predescribed area of natural habitat, are probably impossible at the present state of the art." The goal of the bird ecologist is, therefore, to come as close as possible to the correct value by using some type of density estimator. The major problem with using density data is that the various methods are not interchangeable, i.e., densities derived by one of the many line transect approaches are not comparable to mapping or mark-recapture data. Indeed, the cry for some type of standardized approach is justified. The dominant theme of the papers in this section is that various methods discussed are fraught with errors (e.g., Hildén's paper). Is it possible to measure density?

In his introduction to the section on "Comparison of Methods," Robbins states that we should view the papers with the objectives of determining ". . . which method or combination of methods may be best . . ." The problem with that is to what do we compare the method in question? To another method as in the Franzreb; Edwards et al.; Anderson and Ohmart; O'Meara; Redmond et al.; Tilghman and Rusch; or Svennson papers? Or to some "parameter" of population based on intensive sampling as in the DeSante paper? The problem with the first approach is obvious, you have no real density upon which to base your test (see for example Tilghman and Rusch who determine bias in estimators by comparing them to their ". . . best estimate of actual bird density."). The problem with the second is that by the time you use ". . . an intensive program of color banding, spot-mapping, and nest monitoring" to determine your parameter who knows what your variable circular plot technique will show? Surely there must be some investigator effect. However, I can think of no good way to improve on DeSante's approach and clearly it gives better results than the others in this section. I don't think there is a satisfactory way to determine which method is best.

The next three sections, totaling 25 papers deal with sources of variability (and ultimately error) in sampling techniques. Just about every possibility is covered with the most intriguing being the extreme likelihood that investigators hearing ability decreases with age, thereby biasing censuses that rely on aural cues. And although the Ramsey and Scott recommendation that all potential field workers have their hearing tested before sampling is not cost effective nor even practical in most situations, it would definitely seem warranted based on their sample of 274 (including myself) symposium attendees.

I feel the real meat of the symposium lies in the next two sections on sampling design and data analysis. Although some of the papers in these two sections require a little mathematics (e.g., the papers by Gates, Pollock, and Johnson), the material should not be viewed as too hefty and if the reader will expend a little effort the reward is great. One wonders why the Burnham et al. paper was published in this symposium when most of the material is already covered in their 1980 Wildlife Monograph.

The last section, "Overviews," seems to be a catch-all for papers that didn't fit too well into the other sections. Wiens paper makes a good point about the pitfalls surrounding "single-sample surveys" and advises the reader about types of scale problems (e.g., space and time) inherent in bird population sampling. Anderson effectively summarizes the often mis-used approach of using multivariate statistics to correlate habitat variables and bird presence (not habitat selection as some might think). Appropriately enough, the symposium is summarized by John Emlen who, recognizing all of the sources of error, maintains that the methods presented should be ". . . promoted for the present as the best we have been able to devise." That is not to say, however, that research into techniques should decrease.

I recommend this symposium to all bird ecologists with the caution that just because it's said in print doesn't make it true. My only major complaint is about the study organism to which this symposium is directed. Is it birds or avians?—Robert C. Whitmore.

Mate Choice. By Patrick Bateson (ed.). Cambridge University Press, Cambridge, United Kingdom, 1983:xv + 462 pp., text figs., tables, and black-and-white photos. $59.50 (hard cover), $19.95 (paper cover).—This book is a collection of papers presented at a conference on mate choice held at Cambridge in July, 1981, to which have been added some "specially commissioned" chapters. As with many such edited volumes, the result is very much a mixed bag. Broadly focussed literature surveys mix with narrowly focussed reviews, empirical studies with theoretical models, and exciting chapters with dull ones. There is even an admixture of the completely irrelevant (e.g., W. Wickler and U. Seibt on "Monogamy:

an ambiguous concept"). The editor states in his preface that the authors "re-wrote their papers as surveys rather than as presentations of new data." Accordingly, few new results are included, and when a new result is reported we are often not shown enough data to evaluate its validity. Nevertheless, many of the chapters are useful as summaries of the literature, and some new ideas and interpretations are introduced.

One useful feature of the volume is the presence of non-technical treatments of various mathematical models of the evolution of mate choice. P. O'Donald discusses his major gene models, in which both female preferences and the attractive male traits are controlled by single loci; S. J. Arnold discusses R. Lande's polygenic models, in which both preferences and attractive traits are controlled by many loci; and G. A. Parker discusses his ESS models, which seek to determine what mixture of male and female choosiness will be proof against invasion by mutant strategies. These three chapters all provide easily-understood summaries of sophisticated modelling efforts. Less successful are R. I. M. Dunbar's superficial rehashing of life history theory, and M. Petrie's rambling discussion of mate choice in species showing sex role reversal. A chapter by J. F. Wittenberger on decision making strategies in mate choice adds little to the earlier work of A. C. Janetos.

Several chapters will be of particular interest to ornithologists. I. Rowley provides an innovative review of re-mating in birds that also serves as a good introduction to the literature on the breeding ecology of Australian species. F. Cooke and J. C. Davies summarize the superb work on assortative mating by color phase in the Lesser Snow Goose (*Anser caerulescens*). J. C. Coulson and C. S. Thomas give an update on the long-continuing work on mate choice in the Kittiwake Gull (*Rissa tridactyla*). A chapter by J. B. Hutchison and R. E. Hutchison demonstrates that, surprisingly, something is known about hormonal control of mate choice in birds. By contrast, J. W. Bradbury and R. M. Gibson's chapter emphasizes how little is known about mate choice in lekking birds, despite years of effort by researchers.

Several papers reflect the interest of the editor, P. Bateson, in optimal outbreeding, the idea that mate preferences are a compromise between the need to avoid inbreeding depression and the benefits of preserving local adaptation and coadapted gene complexes. Under this hypothesis, individuals are expected to prefer mates that are "a bit different but not too different" from close relatives. Bateson's summary of his own work with Japanese Quail (*Coturnix coturnix*) provides some empirical support for the hypothesis. However, L. Partridge's thorough discussion of the genetic consequences of mate choice turns up little evidence of harmful genetic effects of outbreeding. Moreover, the review of mate choice in Snow Geese by Cooke and Davies demonstrates how species isolating mechanisms can lead to apparent outbreeding avoidance within a species, and B. D'Udine and E. Alleva's discussion of preferences of house mice (*Mus musculus*) for familiar versus unfamiliar individuals illustrates how widely the preferred degree of familiarity can vary depending on the strains, traits, and rearing procedures used in the experiments.

Emphasis throughout the volume is on mate choice based on genes, with little attention to choice for mates that possess good resources or that will make good parents. Taxonomic coverage is also patchy; studies of birds and mammals are emphasized while fishes and insects get short shrift. Taken together, the book provides a good introduction to some, but not all, of the active areas of research on mate choice.—William A. Searcy.

John Gould—The Bird Man: A Chronology and Bibliography. By Gordon C. Sauer. University Press of Kansas, Lawrence, Kansas, 1982:xxiv + 416 pp., 36 color plates, 80 text figs. $65.00.—It is surprising that a satisfactory biography of John Gould was not written in the century following his death (1881) in view of the fact that "In the field of natural history the accomplishments of this man in his 76 years of life from 1804 to 1881 are truly

monumental. No other ornithologist has ever exceeded (or will ever exceed) the number of Gould's bird discoveries and the magnitude and splendour of his folio publications." (Quoted from the introduction to the present volume.) The work reviewed here is also not a biography but rather a comprehensive compendium of biographical and bibliographical information. As such it goes a long way toward filling the biographical void. Gordon Sauer has been pursuing the story and myth of John Gould for nearly 40 years and has accumulated an enormous amount of information found scattered over three continents and locked away in dusty (!) museum archives. It is to his credit that this information is now compiled and accessible to others, particularly in view of the current interest in the history of ornithology and in bird art and illustration.

The book is divided into four major sections: (1) genealogy (8 pp.); (2) major published works (54 pp.); (3) chronology of life and works (68 pp.); and (4) bibliography (235 pp.), plus a comprehensive index (22 pp.). Parts (2) and (3) are profusely illustrated with black and white reproductions (67 of the 80 text figures illustrate these sections). The 36 excellent color reproductions of original drawings by Gould and others are spread throughout the book, further illustrating the text as well as adding considerably to the aesthetic quality of the work.

The section on genealogy is short, being two standard tables covering the Gould and Coxen families starting from John and Elizabeth [Coxen] Gould's paternal grandparents and continuing to the present. The short (2 pp.) introduction acknowledges the sources of much of this information.

Part (2), "John Gould's major published works," is a careful and thorough conspectus of the 30 most prominent of Gould's many publications. For each work the following topics are discussed (where applicable): prospectus; number of plates; dates of publication of the parts; contents of the separate parts; reviews. Sauer has examined many copies of each of the works and has especially benefitted from the Ellis collection at the University of Kansas, by far the largest single collection of Gould materials in existence. Much original scholarship is evident in this section; some of Gould's works are collated for the first time (the unique Ellis material, often in original parts as issued, was indispensable). It is surprising, given the prominence of the Gould folio works, how much is unknown regarding these publications. For example, precise dates of issue for the various parts of some works are not known nor is the number of plates in each part in some cases. A considerable number of published bibliographic errors are identified and (where possible) corrected, and Sauer indicates a number of avenues for further research. In addition, this section is a gold mine of notes on specific sets of Gould's works as well as various letters, unpublished manuscripts, and other pertinent bibliographic material.

Part (3), "chronology of the life and works of John Gould," is the raw material of a biography. The brief (2 pp.) introductory text provides a concise historical context of Gould's time by listing a number of facts pertinent to his development and career (e.g., extant printing methods, modes of transportation, attitudes about birds, etc.). The chronological list includes all important events in Gould's life as well as a great many minor ones. Also included are numerous references to Gould's relatives and associates and to the ornithological community of the time. The list is profusely illustrated with black and white figures as well as excerpts from many letters from, to, and about Gould.

The final section (and at 235 pp., by far the longest) is a bibliography of John Gould, his family and associates. It appears on the surface to be an alphabetic list of every book, manuscript, article, or other printed work (and some not printed) bearing any reference whatever to John Gould. It is quite a list and a number of the entries seem only just faintly relevant. I would have preferred a more complex organization, with at least some judicious separation of the more minor references into a separate section. However, there are many possible organizations and it was, perhaps, not clear which would best serve Sauer's audience.

Sauer has included information in this last section on a large number of unpublished items including original drawings attributed to Gould or his artists, miscellaneous correspondence, and manuscripts. As always throughout the book, complete sources of these materials are given. The sections pertaining to Gould in several major bibliographies of ornithology (e.g., Zimmer 1926, Wood 1931, Anker 1938) are reproduced in their entirety, a useful inclusion since some of these works are now difficult to obtain. Also included are quotations (some extensive) from important and/or obscure sources. Finally, a number of major references are thoroughly indexed (with respect to Gould and his associates) for the first time. Among these are Whittell (1954. "The literature of Australian birds"), Palmer (1895. "The life of Joseph Wolf"), and several journals (Emu, Ibis, etc.).

The book concludes with a carefully compiled (no surprise at this point) comprehensive index. If one must find a flaw it is that Latin names are indexed only by genus. Most important in the index are the names of people mentioned in the text; as far as I can tell, none are missed. It is nice to see such care taken on a section of such significance to a book so filled with facts and names.

Gordon Sauer is (by his own admission) neither a bibliographer nor an ornithologist and he is not yet a biographer. He has, however, amassed and compiled an enormous quantity of information on the life and works of John Gould. A few ragged edges occasionally show but historians of science, future biographers, and anyone interested in this larger-than-life man owe a great debt to Sauer for his efforts. We must thank him for making the information available rather than hoarding it for another decade or two until a more polished (perhaps) version could be produced.

This book is not for everyone. It cannot be easily read like a novel; there is far too much raw data—overwhelming. As a gold mine of information on not only Gould but also many of his contemporaries, this book is a must for anyone seriously interested in the history of ornithology or in zoological illustration. It belongs in every major library. I now look forward to the next steps (already suggested and outlined by Sauer as projects for himself and others) incorporating new information and interpreting the present data to produce a more integrated picture of the life of John Gould.—D. Scott Wood.

The Birds of Africa. Vol. I. By Leslie H. Brown, Emil K. Urban, and Kenneth Newman, with illustrations 1–17 by Peter Hayman, 18–32 by Martin Woodcock. Academic Press Inc. (London) Ltd., London, England, 1982:xiv + 521 pp., 28 color plates, 4 black-and-white plates, 9 figs. of which three are maps, two tables. £53.40 ($99.00).—This is the type of handbook I wish I had had 20 years ago when I lived in Africa. It would appear that the front flyleaf comment "These volumes are sure to be acclaimed as the authority of the avifauna of Africa for many years to come" will be a reality. The first hope of the authors is certainly fulfilled by filling a need for "a comprehensive handbook." I trust that the other two hopes will be realized viz. to pinpoint further study subjects, and to stimulate "much needed research" on the African continent.

The planned four volumes will cover 1850 species. In Volume I there is a well written, readable comprehensive introduction of 29 pages. It is unfortunate that Brown's death on August 1980 has curtailed some of the preparation and research, but certainly Urban and Newman are to be commended on a job well done. The introduction is laid out under three headings: the main Features of African Bird Faunas, including the Geological Past, Climate, Vegetation, Habitats, Kinds and Numbers of Birds in Africa and Bird Movements Within Africa. The next section deals with Some Possibilities for Research, namely, Systematics and Distribution, Nest and Eggs, Breeding Seasons, Voice and Song, Daily Routine and Energy Budgets, Food and Feeding Methods, Ringing, Marking and Migration Studies,

Numbers and Census Data, Pesticides, and Longer Term Studies. The third section covers Scope, Contents and Layout of the text, dealing with Existing Reference Works, Scope of the Book, Nomenclature and Systematics, Ranges and Status, Descriptions, Field Characters, Voice, General and Breeding Habits, and References. There follows two pages of general references. The parts of African birds are drawn on two unnumbered pages. This seems to be redundant especially since most handbooks include it. The main text covers 447 pages. The bibliography is given in three parts: general and regional references (consulted for all families), references for each family, and sources of sound recordings. The indexes gives scientific, English, and French names.

Almost every species is illustrated on the 28 color plates. The illustration of sex, immature plumages and color phases are a needed and useful addition. I can well remember submitting color drawings of hawks to the late C. W. Benson whose only comment on returning them to me was "excellent drawing, but I don't know to what species they refer." The line drawings are interesting and portray typical behavior patterns. The head drawings of birds of prey are most useful. The four black and white plates of birds of prey as seen overhead are diagnostic and will prove very useful. There are maps for every species and these appear to be very accurate. One could wish that the eggs had been illustrated, but the task would be an immense one.

One learns that of the ca. 1850 species none is resident in every part of Africa. Twenty-five endemic species, four essentially montane are found in Ethiopia. About 50 species are irregular or vagrant visitors; ca. 95 species are regular visitors that do not breed; ca. 90 species are Palearctic land birds, which have breeding populations in north Africa and winter in the tropics; 165 Palearctic land birds have breeding populations in northwest Africa, but do not breed into sub-Sahara Africa; 1450 species are residents south of the Sahara in the truly Afrotropical region and two orders, Coliiformes and Struthioniformes, are endemic to this region, as are 13 families and subfamilies. Much could be said about the variations of Palearctic migrants that come into Africa.

The species accounts of necessity are variable, relating to our existing knowledge of each kind of bird. Terms such as "intimately known" and "little known" will tell the reader immediately concerning the ecological and behavioral aspects of the individual species biology. I found the account of the Ostrich (*Struthio camelus*) very fascinating. The nest-building and courtship of the Hamerkop (*Scopus umbretta*) should be read by everyone. The accounts of the African Open-bill Stork (*Anastomus lamelligerus*) and the Marabou Stork (*Leptoptilos crumeniferus*) were of special interest since I have studied colonies of these, and observed hundreds of them. I read the accounts of 20 birds of prey with great interest and learned a great deal.

Naturally in a work of this scope some data would appear to be missing. From my own background in Africa I wondered why no mention was made of the White-necked Cormorant (*Phalacrocorax carbo*) using live sticks with green leaves on them in nest-building, or the Long-tailed Cormorant (*Phalacrocorax africanus*) using trees for nesting as it does in southern Malawi. One wonders why the Malawi breeding dates were left out for the Marabou Stork, or why little was said concerning the movements of Pink-backed Pelicans (*Pelecanus rufescens*).

The authors have used the sequence of Voous' "List of Holarctic Bird Species" (1973–77) and his proposed sequence in the forthcoming edition of "A New Dictionary of Birds" by Campbell and Lack, for orders and families. In certain instances, e.g., Falconiformes, the authors' arrangement is followed. Generic and species names follow Hall and Moreau (1970) and Snow (1978) for species south of the Sahara. Areas not covered by these follow Peters et al. (1934–79). I hope that these volumes will become a standard in systematics for a number of years. I have at least four systems in my African library!

The authors and publishers are to be congratulated on a job well done. If the remaining volumes live up to the standard of Vol. I, there is not a doubt that the authors' dreams will be fully realized. Unfortunately in the copy I received pages were coming loose. It does seem a shame with such a high price that better binding was not possible. The price will be too high for many. One can only trust that most libraries will purchase the series.—R. CHARLES LONG.

ONCE A RIVER. By Amadeo M. Rea, illus. by Takashi Ijichi. University of Arizona Press, Tucson, Arizona, 1983:285 pp., 30 figs., 15 distribution maps, 14 tables. $24.50.—According to the author, this book has three major functions: to provide a regional account of the bird life of the Gila Indian Reservation and adjacent areas, to focus on the migration of birds through this section of Arizona, and to provide a study of the avifaunal changes within the past century. In addition, the book provides an excellent historical account of habitat changes along the Gila River and an interesting historical and ethnographic account of the Pima Indians.

The book is divided into two sections: "Changes on the Middle Gila," which includes most of the above topics, and "Species Accounts," which emphasizes the regional account, migration, and ethnographical aspects. As well as subject matter, the two sections differ in style. The first is a mostly descriptive, easy-to-read, informative account which will appeal to a wide audience. The emphasis is as much on habitats and history as on birds. The second section is more technical. Most of it, which is more than half of the book, is composed of species accounts. From a strictly scientific standpoint, the first chapter of this section is the meatiest. Here, the author expounds upon his views on taxonomy and his philosophy of ornithology as a science. Birds are mentioned only by latin names, not common names as in the rest of the book. Because of the subject matter and its treatment, this part will appeal mostly to ornithologists, though the ethnographical accounts should be interesting reading for almost anyone.

Overall, "Once A River" fulfills its functions well. The first part, especially, is a well-written account of habitat and avifauna changes in central Arizona and provides an excellent documentation of the sorrowful destruction of riverine and riparian habitats. It is this section that sets this work apart from the typical regional bird book. It serves well to remind us of the drastic changes that have occurred in the Southwest after the arrival of European man. The 244 species accounts are more interesting than those in most regional works because of the inclusion of sections on archaeology, ethnography, history, and taxonomy as well as the usual modern status and the expected section on change in status.

Problems that I found with the book were the overall lack of quantitative data and the sometimes inadequate documentation for some of the conclusions. Emphasis is on presence or absence of species and population statuses are usually described only by such terms as "common" or "a few pairs." When population sizes are given, no area is specified and densities cannot be ascertained. Though we are told that the author spent over 1000 days in the field over a 20 year period, we are not told at which seasons and in what habitats they were spent. These are important omissions when conclusions are made about changes in population sizes, changes in wintering status, changes in departure times of winter residents, and, to a lesser degree, local riparian recovery. Though few quantitative data were provided by earlier ornithologists for comparison, the author could have provided some for present and future comparisons. Though this lack of quantitative data and documentation does not usually detract from the veracity of the author's conclusion, it is emphasized by his own careful distinction between "birdwatching as a pastime and ornithology as an empirical science." His statement that "science must be based on verifiable evidence pre-

served for reexamination" also contrasts with his extensive use of the notes of early ornithologists and ethnographic accounts. Are these accounts of no ornithological value because there is no specimen for each observation?

The only glaring error I found in the book was the author's statement that his discovery of Orange-crowned (*Vermivora celata*), Black-throated Gray (*Dendroica nigrescens*), Townsend's (*D. townsendi*) and Hermit (*D. occidentalis*) warblers in November 1977 constituted the first winter records for southern Arizona. All of these species had been recorded years earlier on Christmas Counts and Orange-crowned and Black-throated Gray warblers were almost regular. But then, perhaps these were not considered to be "empirical" observations.

The above criticisms pertain to a relatively small section of the book and the problems described do not detract appreciably. They will be of little importance to most readers. This book is excellent reading material for anyone interested in the environment or Arizona history, and is a valuable contribution to our knowledge of Arizona birds.—G. Scott Mills.

South American Landbirds, a Photographic Aid to Identification. By John S. Dunning. Harrowood Books, Newtown Square, Pennsylvania. 364 pp., 1200+ color photographs. $37.50; soft cover $32.50.—Those of use who are becoming accustomed to seeing the comprehensive and detailed field guides entering the marketplace with regularity, dealing with various geographic regions (National Geographic Society: North America; de Schauensee & Phelps: Venezuela) and also specific groups of birds (Harrison: seabirds) might be somewhat disappointed in Dunning's book. So would those who are looking for the definitive guide to South American birds, covering in a more detailed and comprehensive fashion, most, if not all of the diversity of species on that continent. In this case, the days of carrying two, or even three or more, books to use in the field in many areas of South America have not yet ended, if indeed they ever will.

But, as every year goes by, the literature on the avifauna of South America grows, and the Dunning book is a fine contribution to add to the resource list of that continent's birds. In conjunction with field use of such regional guides as that for Venezuela and the forthcoming Colombian book, it will prove useful and educational. More appropriately, the almost overwhelming array of photographs (illustrating over 100 species of hummingbirds alone!), of consistently high quality and often illustrating little known birds, or characteristic birds of seldom travelled avifaunal areas, will appeal to all naturalists interested in the richness of bird life of the Neotropics. About 1100 species of birds are illustrated in this book, usually 12 to a page. The photographs are rather small in size, usually about 1½″ × 1½″.

The 1100 species represent less than half of the known South American landbirds. The remainder are covered in the second half of the book, and are described only. The term "landbird" is somewhat loosely applied, as there are photographs of Cattle Egret (*Bubulcus ibis*), Spotted Rail (*Rallus maculatus*), and some waders. Some groups are well represented, particularly tanagers, of which over half the known species are illustrated. In contrast only 21 species of parrots are illustrated. However, parrots are obviously more difficult to capture for photographic purposes using Dunning's technique, and this explains why this family and several others are relatively poorly represented. Of the parrot photographs, six are by Robert Ridgely, the book's collaborator, who also contributed about 30 other photographs.

It is unfortunate that none of the species of diurnal raptors were represented by flight shots. While there are many good photographs of species of ovenbirds, antbirds, and flycatchers, unfortunately not enough of these species are illustrated. In my copy, some of the photographs seem to have suffered in reproduction. For example, the Slate-colored Grosbeak (*Pitylus grossus*) 176-11 appears too greenish and the blue cap of the Blue-hooded Euphonia

(*Euphonia musica*) 174-4, seems to have been re-touched to a more vibrant shade of blue. There also appear to be some misidentifications. The obvious ones are the apparent transposition of the elaenias on p. 110, numbers 5 and 6, and the female Barred Becard (*Pachyramphus versicolor*) posing as a Dusky-tailed Flatbill (*Ramphotrigon fuscicauda*) on p. 112, number 4. Other apparent misidentifications have been described elsewhere (Parker, Auk 100:775, 1983).

The descriptions of all the species cover plumage characteristics and are generally well done as is the layout of the book and the typography. While no information is given on habits, vocalizations, or behavior, an alphabetical coding system is used to identify species' elevational zones and preferred foliage types. Beyond the plumage characteristics, a substantial lack of other relative information limits field identification usefulness, particularly for those species for which there are no photographs. A chapter on the methods and equipment John Dunning used in his field photography is also included. My hardcover came with an addenda and corrigenda to some of the descriptions.

Each species description also includes a rather small range map. From experience in trying to use these maps in the field, I have found their accuracy somewhat wanting. For example, on planning a recent trip to the forests of southeastern Brazil, I was unable to satisfactorily determine if I could expect to see the Striped Manakin (*Machaerpterus regulus*) in the Brazilian state of Minas Gerais. However, the endpaper maps in the hardcover edition might be useful in interpreting distribution a little more precisely. Quality of these maps has also been described elsewhere (Parker, Auk 100:775, 1983).

As a contribution to ornithological literature on the broadest scale Dunning's book is excellent and most welcome. It deserves the support of everyone—from the professional ornithologist to the casual bird observer. (Ten percent of the publisher's sales receipts are to be donated to the World Wildlife Fund-U.S., to be used for the purchase and protection of bird habitat in South America.)

The purpose of the book seems somewhat ambivalent. Dunning introduces it as being "designed to help the beginning bird-watcher identify the land birds of South America . . . through photography." Yet he also states that "the basic reason for this book, . . . is to try to interest more people in the battle to save habitat" (in South America).

In my view the book may not serve the novice birder as well as it could, without suitable cautions, and perhaps could serve a general audience better if the product were presented or packaged a little differently for that audience.

Identifying birds in the field has come a long way in the last 20 years, with the improvement in resources, guides, equipment, knowledge, and logistics. With these advances, has come a direct improvement in the identification skills of experienced field ornithologists who now go far beyond traditional field mark techniques before identifying a bird. They evaluate voice, behavior, habitats, distribution, and an ephemeral quality the British birders call "jizz" which can loosely be defined as a "combination of everything!" This latter characteristic can often be captured through a series of paintings or by a particular painter, but it is a very difficult quality to replicate in photographs. Photographs, even a series of them, often "freeze" a bird under a particular set of conditions and often, those conditions while not totally artificial, are not entirely the ones under which the bird might be normally observed. The representation of birds in the photographs in Dunning's book have to be evaluated in terms of lighting, backgrounds, poses, focus, apparent feather damage (from mist-netting), and production processes. The latter has resulted in the severing of some bills and tails and some apparent color-bleeding. Thus to translate a field observation, particularly in South America, where often the vicissitudes of lighting conditions, species behavior, and habitat magnify observational difficulties, to a positive identification using photographs (even those as good as Dunning's) requires wariness on the part of advanced field observers, let alone novice birders!

On the other hand, interesting more people in preserving habitat in South America might work better if the book were aimed at a wider audience. I think the book can stand alone, as a photographic essay. In this sense, the second half of the book, consisting of descriptions of unphotographed species, could have been omitted, and the descriptions for the photographs presented more generally, rather than describing plumage characteristics alone.

Having had time to examine the book a little more closely, one might also come away with the feeling that John Dunning may have simply tried to accomplish too much. Combining a photographic review of bird species of the world's greatest bird continent and aiming it at a general audience, along with trying to develop a fairly comprehensive guide for use by the field ornithologist, seems more than difficult. But this is understandable, given that it is a reflection of John Dunning's personal love, accomplishments, and contributions to knowledge of South American avifauna.

All naturalists will enjoy scanning the pages of this interesting book to view the remarkable variety, color, and form of South American birdlife. I for one, appreciate being able to add this volume to my collection and to view at leisure, species of birds which I may never be able to see in the wild. At the field level, observers (particularly beginners) need to be aware that for best results they should use the book in conjunction with current published regional guides and that the photographs as identification aids should be employed with discretion. However, if one is visiting an area in South America for which no good guide now exists, this book will prove an excellent starting point.—Lou Marsh.

Hawaii's Birds, 3rd Edition. By Robert J. Shallenberger (ed.). Hawaii Audubon Society, Honolulu, Hawaii, 1981:96 pp., numerous color photos, paintings, and maps. Paper cover. $3.95.—The latest edition of this attractive and compact guide is a must for birders in the Hawaiian Islands, and a useful brief introduction to the Hawaiian avifauna. It includes sections on marine birds, waterbirds, urban birds, upland birds, and forest birds. For each species there is a brief text covering distribution, description, voice, and habits. Each species is illustrated in color, either by a clear photograph, a reproduction of a painting from the classic Rothschild monograph of the turn of the century, or an attractive new painting by H. D. Pratt. A table gives the abundance of each species in various habitats, and there are lists of migratory birds, introduced birds, and selected references. Maps of birding locations are provided for the islands of Kauai, Oahu, Maui, and Hawaii. The book may be ordered by mail from the Hawaii Audubon Society, Box 22832, Honolulu, HI 96822. Add $0.70 postage for surface delivery or $1.03 for air mail.—R.J.R.

Breeding Birds of the Baraboo Hills, Wisconsin: Their History, Distribution and Ecology. By M. J. Mossman and K. I. Lange. Wisconsin Department of Natural Resources and Wisconsin Society for Ornithology, Madison, Wisconsin, 1982:198 pp., ill. Price not given.—This is much more than an annotated list of the breeding birds of the Baraboo Hills—a small but relatively undisturbed area in southern Wisconsin. A major focus of the book concerns a detailed analysis of avian habitat requirements, resulting from transect surveys on 77 stands in the hills, accompanied by detailed habitat sampling within the territories of birds. Habitats selected by each species with respect to parameters measured, and a discussion of habitat differences among various members of several foraging guilds are given. Statistical comparisons are set out in a number of easily understood figures and tables.

Maps and descriptions of the study area, a listing of species characteristic of various

habitat types (forested and more open), a comparison of census results with those of previous authors who worked in southern Wisconsin, the results of phenology studies, a discussion of changes in land use patterns, and previous ornithological work in the area, plus qualitative information on changes in the avifauna since settlement compliment the above discussion, as well as contribute to an historical perspective.

An equally large portion of the book is then devoted to accounts for all species which have been found in the hills in the month of June, a limitation that I found attractive. The accounts present information on distribution, abundance (present and historical), arrival and departure dates, location and timing of nesting events, and the habitat associations for each species. Also included for each species is a list of other birds that were noted as being closely associated during transect counts. This offers a first step in an attempt to understand changes in habitat selection throughout a species range, and the factors that may contribute to such changes.

A discussion of the conservation needs for the Baraboo Hills, descriptions of birdwatching spots, a summary of breeding information for each species, descriptions of transect count areas with the specific results of those counts, and a bibliography "round out" the work. There are a number of photographs of people and places, that add a pleasant touch.

Nomenclature generally follows the 1957 AOU Check-list, but there are a number of exceptions and no standard is cited. The inclusion of Reeve's Pheasant (*Syrmaticus reevesi*) under "extinct and extirpated" seems somewhat unusual. In general, the text appeared to be free of errors, except for headings in species accounts (Vieillot is misspelled on pages 81 and 102, as are *sialia* and *pedioecetes*). A figure on page 8 is printed upside down, and the reproduction of one map and an aerial photograph is rather poor. However, these do not detract greatly from the overall usefulness of the publication. The authors seem to have met their objectives of documenting the value of the region for study as well as contributing to and understanding of species-habitat interrelationships. I would recommend this work to anyone interested in similar studies or in the bird life of the southern Wisconsin area.—R. D. James.

A Guide to the Birds of Puerto Rico and The Virgin Islands. By Herbert A. Raffaele. Fondo Educativo Interamericano, San Juan, Puerto Rico (available through Addison-Wesley Publishing Co., Reading, Massachusetts 01867), 1983:253 pp., 24 color plates, 15 illustrations, 2 tables, 9 maps. $13.95.—The "Introduction" presents the author's goals, an explanation of how to use the book, a discussion of the composition of the avifauna and a short discourse on field hazards—of merit as a warning to the unwary birder. Biogeography of the islands is discussed and the uniqueness of the area is made known by the author. Conservation is covered quite thoroughtly because this is island avifauna and its conservation cannot be stressed enough. A table of endangered species and what may be contributing to their demise is included at the end of this section.

The plates are generally representative of the species they are intended to depict, with a few exceptions. The Spotted Sandpiper (*Actitis macularia*) (p. 11) should have flesh-colored legs, and the Pearly-eyed Thrasher (*Allenia fuscatus*) (p. 30) has a tapered and pointed lower bill; it does not terminate abruptly as shown.

The flying waterfowl (p. 17) appear to have the browns washed out making them appear too light, the Red-legged Thrush (*Turdus plumbeus*) (p. 30) has too much of a blue tinge on the upper breast and belly, the Yellow-shouldered Blackbird (*Agelaius xanthomus*) (p. 36) has a black bill which does not show up in the plate, the Puerto Rican Tanager (*Nesospingus speculiferus*) (p. 37) is darker brown on the dorsal surface than is shown.

While leafing through the "Biogeography" section for a second time pages 15 through 24 literally fell out of the binding. It is unfortunate that a reviewer gets a copy that may be

atypical of the product. However, as a field guide this book will get more abuse than simply being leafed through, so the binding may be a problem.

The species accounts are interesting, especially the comment sections which provide up to date vignettes of the biology of each species. Unique to this field guide is a section (pp. 199–213) with maps showing specific "places to bird" on the islands. This section is followed by a locality checklist (pp. 216–230) in tabular form.

Anyone planning to study birds in Puerto Rico or the Virgin Islands will find this book a valuable and informative guide.—James A. Dick.

The Birds and Birdlore of Samoa: O Manu Ma Tala'Ago O Manu O Samoa. By Corey and Shirley Muse. University of Washington Press, Seattle, Washington, 1983:x + 156 pp., 76 color photographs, paintings, maps. $15.00 (paper).—The authors of this book, a husband-and-wife team who spent 6 months in Samoa gathering material, wanted to write a guide that would be useful both for visitors and for the native Samoans. This aim is a laudable one. Unfortunately the result falls short of its goal in many ways.

An introduction provides a brief and incomplete ornithological history of Samoa, and a concise account of the geography of the islands with maps of the group. Unfortunately the maps have been reproduced at too small a scale and are difficult to read. The bulk of the text is taken up with species accounts, interspersed with native legends and proverbs about birds or featuring them. The species accounts are grouped under four headings: seabirds, migratory birds (northern-hemisphere shorebirds and the Long-tailed Cuckoo [*Urodynamis taitensis*]), waterfowl, marsh and land birds, and accidental occurrences. The last category documents sightings by the authors of Laughing Gull (*Larus atricilla*) and Common Sandpiper (*Actitis hypoleucos*), species previously unknown from the region. A concluding section includes a checklist, pronunciation guide to Samoan, and "Suggestions for Successful Birding in Samoa"—not bird-finding information but a guide to local etiquette.

The introductory and concluding sections are the best parts of the book. Most readers, however, will be interested in the species accounts and the illustrations. The accounts give brief descriptions of each species, with notes on habitat and local distribution. Unfortunately they suffer from a vague and often confused style. The description of the Red-tailed Tropicbird (*Phaethon rubricauda*), for example, sounds like a bad translation from another language: "The entire bird is white except for a black spot before the eye and a black shaft of the wing feathers." So little has been recorded about Samoan birds that I wish the authors could have been more precise with their descriptions of behavior. Telling us a song is "delightful" informs us about the authors' preferences but gives us no real information about the bird, for example. There are some useful, if highly qualitative, bits of information here but the authors, in their desire to avoid becoming too technical, have gone too far in the other direction. Furthermore, the numerous misspellings of scientific names (e.g., "Meliphagidae," "*Lalagi*," "*faciatus*") do not inspire confidence.

The illustrations are highly variable. The color photographs of many species range from quite acceptable (Blue-crowned Lory [*Vini australis*], Polynesian Triller [*Lalage maculosa*]) to almost useless (Sanderling [*Calidris alba*], Polynesian Starling [*Aplonis tabuensis*]). Seventeen species are illustrated with color paintings by Norman Adams. Most of these are useful for identification, but they are stiff and betray an ignorance of the appearance of the birds in life. The slim figure of the Samoan Broadbill (*Myiagra albiventris*) has little resemblance to the chunky, chickadee-like creature Adams portrays (nor, I might add, to the similarly erroneous figure in DuPont's "South Pacific Birds" [1976, Greenville, Delaware Museum of Natural History], a work the artist seems to have consulted). The fantastic

illustration of the Tooth-billed Pigeon (*Didunculus strigirostris*), a species I have admittedly never seen in life, has the bill totally wrong in both shape and color and fails to show the bare skin around the eye. Samoa's most distinctive bird deserves better in a book such as this.

Although it contains snippets of information hard to come by in other bird books, I cannot recommend this book to ornithologists or visiting birders. They would be far better off spending the extra money required for Watling's "Birds of Fiji, Tonga, and Samoa" (1982, Wellington, New Zealand, Millwood Press), a book with a much more valuable text and vastly superior illustrations. But how does the Muses' book fare as an introduction to birdlife for the local Samoans? I find this point difficult to comment on. I found the various legends and proverbs, all but one of them drawn from previously published works, often difficult to follow or appreciate, but then I lack the cultural background necessary to put them in perspective. However, the Muses' efforts have, I fear, been to a great extent undone by the publishers. If this book is aimed at all at the citizens of a poor country, why pick a format guaranteed to inflate its price? There must be some sort of record that this book breaks for the most white space per section of text or illustration. Of its 156 pages, sixteen are totally blank and nine others have less than a half-dozen lines of text. It is the rare illustration that is bigger than the blank margins surrounding it. Furthermore, why have the publishers chosen to present a book for field use bound along the narrower side, a most inconvenient format? This book could have been half the size at half the price, and then it might have had a real chance of being used by native Samoans. As it is, it is clear that whatever ideas the authors might have had in this direction, they were not shared by the people in the publisher's design department.—Ronald I. Orenstein.

The Hummingbirds of North America. By Paul A. Johnsgard, illus. by James McClelland. Smithsonian Institution Press, Wasington, D.C., 1983:303 pp., 16 color plates, 20 range maps, 6 appendices, glossary. $35.00.—In keeping with the relatively frequent hybridization among hummingbird species, this book is itself somewhat of a hybrid. The first fifth of the book is a quick summary of some aspects of the biology of hummingbirds. This section draws on material about species from throughout the range of this New World family of birds. Much of the remainder of the book is devoted to detailed discussions of the biology of species that breed or have been reported in the United States. Johnsgard also provides a taxonomic listing of all hummingbird species and their ranges, guides to identifying hummingbird species, and a list of "hummingbird-adapted plant" species in North America.

The tremendous research interest in these birds, both for their own sake and as models for general biological problems, has produced an explosion of reports in the last decade that cannot be covered adequately in the first-section summary of the general biology of hummingbirds. The coverage is broad, but also detailed in some aspects of hummingbird biology, especially when hummingbirds are noticeably different from other birds. In general, the material provided is up-to-date, but does not include the full range of biological problems for which these birds are good study organisms. There appear to be only a relatively few mistakes, such as the details of body temperature reduction in torpid hummingbirds.

The second section of the book offers detailed accounts of the biology of species reported from the United States and is the core of the book. This section is a modern treatment somewhat in the style of Bent's life history reports. Included are details of identification, range, breeding, evolutionary relationships, and ecology. The length of this section is expanded by including species that are only vagrants to peripheral areas of the U.S. and for

which rather little is known. However, this does allow Johnsgard to introduce some of the diversity of this primarily tropical family of birds.

The general appeal of hummingbirds has seemed to spawn a number of rather fanciful stories about the behavior of these birds. Some of these are repeated throughout the book, with an apparent acceptance by Johnsgard. However, this book is not designed for the expert in ornithology, but for the amateur, who, along with Johnsgard, may have had a "close encounter" with a hummingbird and has a newly opened interest in these birds. At this level I think the book is an admirable success and I recommend it as good, informative reading.

At first glance this volume may appear to be another "coffee-table" book, but the ratio of text to plates dispels that idea. The plates themselves are generally well-done, although the curvature of the bill of the Green Violet-ear (*Colibri thalassinus*) on the cover jacket could have been slightly greater. Johnsgard is to be commended for having written a book about hummingbirds, rather than having provided some minimal text for a book of pictures of hummingbirds.—Larry L. Wolf.

The Wildfowl of Britain and Europe. By Malcolm Ogilvie, illus. by N. W. Cusa and Peter Scott. Oxford University Press, New York, New York, 1982:vii + 84 pp., 50 color plates, endpaper map. $16.50.—This book is essentially a reprint of the color plates of Anatidae from Volume 1 of "The Birds of the Western Palearctic" (Oxford University Press, 1977; reviewed Wilson Bulletin 93:430. 1981). The endpaper map from the same book has also been re-used here. Page size is the same in the two books, and the color registration has altered very little in the reprint. Stanley Cramp, chief editor of the earlier volume, contributes a brief forward, and the text is by its editor in charge of accounts of breeding biology.

The text consists of a 21-page introduction to the general biology of waterfowl, and brief notes accompanying each plate (usually less than half a page in length). There are no references. The notes to the plates give only a brief description of range, status, field marks of the different plumages, and voice for each species. The general introduction, however, contains a considerable amount of information on individual species. This introduction is a very well-written essay, stressing the variety of waterfowl habitats, diets, and breeding behaviors. A few of the generalizations it contains—such as the statement (p. 13) that "All young wildfowl feed themselves"—are true for European species but are not valid worldwide, but in general the text is a model of concise presentation of biological information for the general reader.

Oxford University Press is to be congratulated on making this excellent set of plates available at a modest price and in a form that will appeal to the amateur birdwatcher, and for accompanying them with a first-rate new text. My only quibble is that the publishers could have included more material from the original handbook, such as the range maps and the outline drawings of different behaviors. They have not stated whether or not this book will be followed by similar volumes drawn from other sections of "The Birds of the Western Palearctic," but I hope that they are considering it.—Ronald I. Orenstein.

Report of the 1979 Greenland White-fronted Goose Study Expedition to Eqalungmiut Nunât, West Greenland. By A. D. Fox and D. A. Stroud (eds.). Nimsfeilde Press Ltd., Aberystwyth, Wales, 1981:319 pp., numerous figs., tables, black-and-white photographs and illustrations. £8.00 from the Greenland White-fronted Goose Study, School

of Biological Sciences, University College Wales, Aberystwyth, Dyfed.—This report documents 1082 man-days of field work in West Greenland focusing on the breeding ecology of the Greenland White-fronted Goose (*Anser albifrons flavirostris*). The Greenland White-fronted Goose winters in the British Isles and its decline in Wales prompted the expedition. One third of the report discusses movements, foraging, and associated behaviors of flocked geese as well as detailed observations taken at seven nests. Two chapters, one on the significance of plumage variation, the other on banding returns would be of general interest. Another third of the book relates general observations on other bird species, mammals, fish, and plants. For the most part, only distribution and abundance are considered, however breeding data are given for about 25 species of birds. As well, there is a study of morphological variation in the atlas vertebrae of caribou (*Rangifer tarandus groenlandicus*) and a chapter on growth in the three-spined stickleback (*Casterosteus aculeatus*). The remainder of the report describes logistical problems and gives personal accounts associated with the 3-month venture in West Greenland.

From the viewpoint of those involved in bird studies in Greenland, the reference list would be a useful addition to a personal library. The notes on trip planning made interesting reading and might be helpful to those considering fieldwork at any isolated high-latitude site.

My two major complaints concern print size—so small that reading is difficult and tiring and secondly, the mixture of anecdotal and scientific reports. A reader interested only in the technical material should be prepared for much browsing. Most likely, only individuals working on White-fronted Geese or on Greenland biota would find sufficient material in this study to warrant a copy in their personal library.—W. Bruce McGillivray.

A Dictionary of Ecology, Evolution and Systematics. By R. J. Lincoln, G. A. Boxshall, and P. F. Clark. Cambridge University Press, Cambridge, England, 1982:298 pp. $47.50.—The authors are staff members of the British Museum (Natural History) working in evolutionary biology. They perceived a need for a dictionary concerned with the vocabulary of scientific natural history, which they term "evolutionary biology," the resultant of overlaps between ecology, evolution, and systematics. This is an advance over the common practice of referring to "natural history" as an outdated synonym of "ecology," and fairly reflects the underlying tone of the work as a whole.

Readers familiar with other biological dictionaries will find this new one to have a fresh and contemporary flavor. This is evident not only in definitions but also in the range of terms included. In common with other biological dictionaries is an emphasis on current, working definitions of terms. Etymology is avoided.

The virtues and deficiencies of a dictionary are determined over time and as a consequence of repeated use. I suspect this dictionary will receive good marks overall. Some terms associated with biology, but which are not biological, are included (e.g., algorithm, heuristic, paradigm), and a few terms that ought to have been entered are not (e.g., isozyme, electromorph). Some terms are only fractionally defined (asymmetry: skewness q.v.).

Having thus demonstated that I did poke around in the corners of the book (one cannot conventionally "read" a dictionary), I must now repeat that it is a good book, with a remarkable range that should satisfy users. I think users probably are college undergraduate and young graduate students. Even so, some old-timers will welcome definitions of what they may suspect to be neologisms. The applications of this dictionary to ornithology are marginal for many users, but persons entering the field could put it to excellent use.—Richard F. Johnston.

SCANS KEY TO BIRDWATCHING. By Virginia C. Holmgren, illus. by Florence M. Walker. Timber Press, Portland, Oregon, 1983:176 pp., 8 color plates, many photos and sketches. $12.95.—Of field guides there seems to be no end and this one is the latest attempt to provide an introduction to bird identification for beginners. The title, SCANS, is an acronym for Size, Color, Action, and Notes the operative words, in that order, of the key on which the book is organized. The user must first place the bird in one of four size classes, by comparison with four well-known birds. The key then leads to the overall color, and hence to cap color followed by breast. At this point only a few species remain and one continues to the bird seen. Unfortunately, while the book attempts to cover all the birds in North America, not all are given in paragraphs. From one to several others are included under a given species as "Look-alikes" or "Close Look-alikes." This system has some unfortunate situations brought about by the too-rigid following of the system. Thus the Black Rail is included as a look-alike of the Lark Bunting—yes it does work out that way.

The write-ups for the various species include descriptions of the color pattern, brief mention of Actions, which is largely a description of feeding habits, Notes, a brief description of the song, and Habitat, described in a few words. A small range map accompanies each. These suffer from the usual faults of range maps. The "Look-alike" species are described very briefly and a brief mention of range is given. There are also 8 color plates illustrating all of the 200 species described. These are a little crude but I think they would be helpful to the beginner.

The system would seem to work well for the species included, especially for the adult males, although females and immatures are included. As a test I successfully keyed out a female Black-throated Blue Warbler (*Dendroica caerulescens*), but failed on a fall Tennessee Warbler (*Vermivora peregrina*) with a green head. The song descriptions are not very helpful: all the warblers are said to have a "sewing machine trill".

Besides the key there are brief sections on "Birds for the record book", "About names and Latin labels", "Inviting birds to your yard", and "For the birdwatchers bookshelf".

All field guides suffer from the necessity of forcing a complex array of information into some kind of rigid system. Learning to identify birds is a complex process, and different people do it in different ways. Mrs. Holmgren's system will not help some people but in general I feel that this could be a useful tool for beginners.—GEORGE A. HALL.

THE BIRDWATCHER'S ACTIVITY BOOK. By Donald S. Heintzelman. Stackpole Books, Harrisburg, Pennsylvania, 1983:250 pp., 72 photos, 8 figs. Paperback. $11.95 in U.S., $14.95 in Canada.—Readers of The Wilson Bulletin will be familiar with the number of recent books aimed at beginning bird enthusiasts. These books describe techniques of bird photography, how to build a nest box, a blind, a better bird feeder, and, generally, what sorts of things to do if bird identification and listing don't give complete satisfaction. The intent of these books, to rekindle an interest in Natural History, is admirable, but the quality varies greatly. Although not without merits, the present volume is not one of the best. The text tends to be superficial, lacking the details and complexities that excite. The reader is frequently told that certain activities are interesting, but, I think, rarely convinced. Parts of the text and a number of photos appear in a similar format in Heintzelman's previous volume on bird-watching, "A Manual for Bird Watching in the Americas" (Universe Books, 1979), to which the author makes repeated reference starting from the third sentence of the preface. In fact, the current volume appears to be a scaled down, slightly reoriented version of the 1979 book.

Recommended projects include: censuses of waterfowl and raptors; nest box construction;

locality studies; breeding bird atlases; bird feeding; and life-history studies (the section on observing nesting behavior lacks any caution about the risks of interference). A thorough and enjoyable chapter focuses on "Collecting Bird-Related Items": bird stamps, decoys, art, autographs, post cards, and shoulder patches. Concluding chapters on conservation projects, and on promotion of bird appreciation are also interesting and of a practical nature. Examples within the text draw strongly on raptors, and, geographically, on locations in the New York-Pennsylvania area.

The book is liberally sprinkled with photographs, mostly Heintzelman's own. The reproduction is not of high quality, but the photos are clear and illustrative and represent one of the strong points of the book, even if many have appeared elsewhere.

There is interesting and well-organized information here. I'm sure beginners would enjoy browsing through it. But since there are some first class books available in the same genre, I must recommend them instead: Pasquier's "Watching Birds" (Houghton Mifflin Co., 1977) is a clear introduction to ornithology; Stokes's "A Guide to the Behavior of Common Birds" (Little, Brown & Co., 1979) is a beguiling approach to bird behavior; Kress's "The Audubon Society Handbook for Birders" (Charles Scribner & Co., 1981) is much like Heintzelman's volume in organization and intent, but far more detailed.—Peter F. Cannell.

Ostrich Index, Vols. 21–50, 1951–1979. By L. P. Phipson and G. L. MacLean. Southern African Ornithological Society, Johannesburg, South Africa: 225 pp. $15.00.—This 30-year index lists English as well as scientific names, but both should be checked as the duplication is incomplete. Authors' names, subject matter, and titles of contributions are also listed, with the latter including entry by different key words. This book is undated, but apparently was published in 1982. A basic reference work for ornithological libraries, it may be ordered from the Southern African Ornithological Society, P.O. Box 87234, Houghton, Johannesburg, South Africa 2041.—R.J.R.

XIX INTERNATIONAL ORNITHOLOGICAL CONGRESS

The XIX International Ornithological Congress will take place in Ottawa, Canada, from 22–29 June 1986. Prof. Dr. Klaus Immelmann (West Germany) is President and Dr. Henri Ouellet (Canada) is Secretary General. The programme is being planned by an international Scientific Programme Committee chaired by Professor J. Bruce Falls (Canada). The program will include plenary lectures, symposia, contributed papers (spoken and posters), and films. There will be a mid-congress free day. Pre- and post-congress excursions and workshops are planned in various interesting ornithological regions of Canada.

Information and requests for application forms should be addressed to:

Dr. Henri Ouellet
Secretary General
XIX Congressus Internationalis Ornithologicus
National Museum of Natural Sciences
Ottawa, Ontario, Canada K1A 0M8

ORNITHOLOGICAL NEWS AND NOTES

COLONIAL WATERBIRD GROUP

The Colonial Waterbird Group will hold its 1984 annual meeting 4–7 October at the Sheraton Inn and Conference Center, Ithaca, New York. Donald A. McCrimmon, Cooperative Research Program, Laboratory of Ornithology, Cornell University, Ithaca, New York 14850, is Local Chairman. Information on submitting applications and abstracts for the scientific program can be requested from William E. Southern, Dept. Biological Science, Northern Illinois University, Dekalb, Illinois 60115.

1984 ANNUAL MEETING

The Sixty-fifth Annual Meeting of The Wilson Ornithological Society will be held at the University of North Carolina–Wilmington, from 31 May–2 June 1984. The University is host for the meeting, to be held concurrently with the Annual Meeting of the Carolina Bird Club. There will be a scientific program, field trips to many interesting sites, workshops of interest to amateur and professional ornithologists, and a spouses' program. Dr. James F. Parnell is chairman of the Committee on Local Arrangements. His address is Department of Biology, University of North Carolina–Wilmington, Wilmington, North Carolina 28401.

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The Wilson Bulletin

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Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, New York 14850.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.

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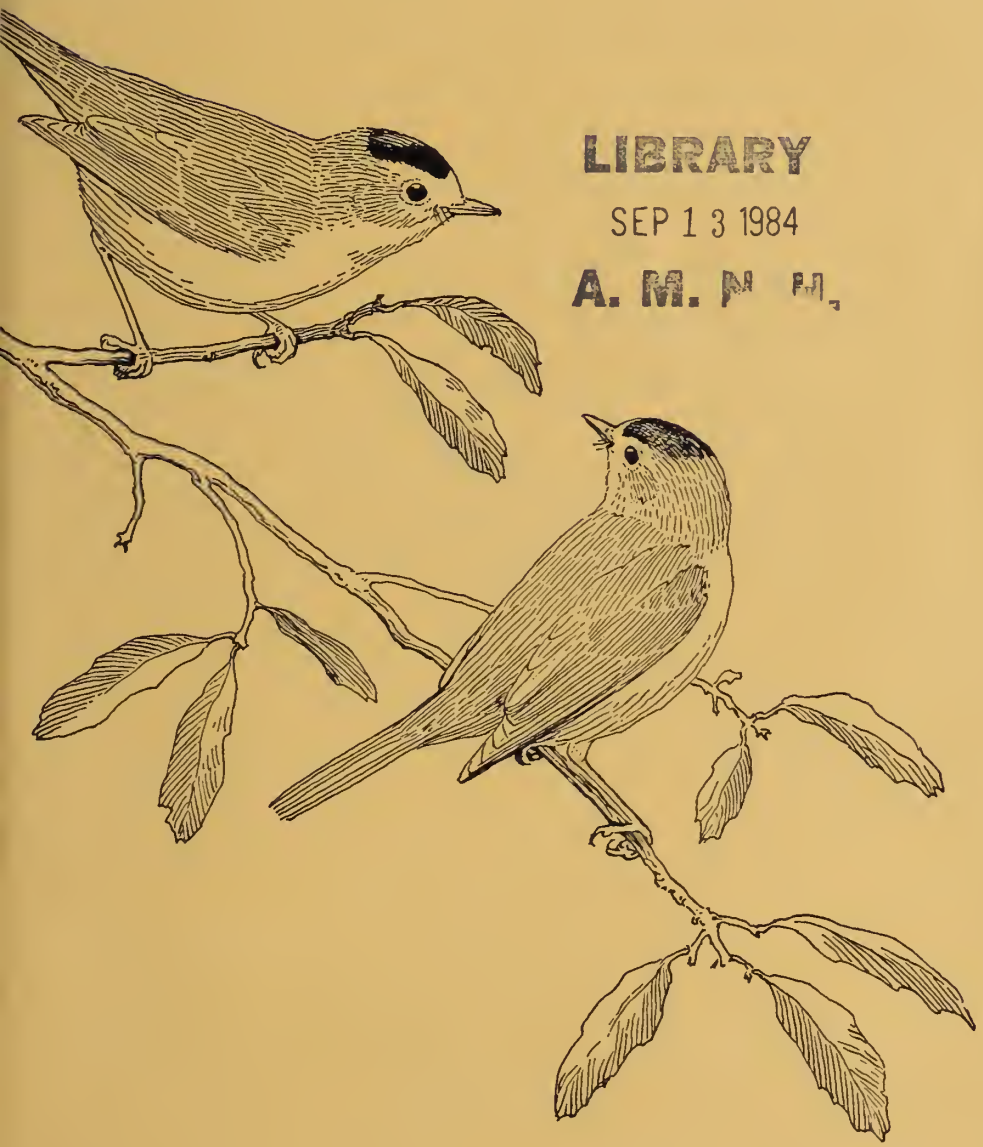

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Adult Sabine's Gull *(Xema sabini)*.
Photographed by Pat Kehoe on East Bay, Southampton Island, N.W.T., Canada.

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PARTITIONING OF FORAGING HABITAT BY BREEDING SABINE'S GULLS AND ARCTIC TERNS

DIANA M. ABRAHAM AND C. DAVISON ANKNEY

Arctic Terns (*Sterna paradisaea*) and Sabine's Gulls (*Xema sabini*) are Holarctic nesting larids which are sympatric in many areas of their breeding range (Godfrey 1966). They are similar in ecology (habitat, nest dispersion), morphology (body size and shape), and behavior (flight characteristics, foraging techniques) (Sutton 1932, Gabrielson and Lincoln 1959, Bannerman 1962). Their diets usually differ: Arctic Terns take mostly fish and Sabine's Gulls mostly invertebrates (Pearson 1968, Lemmetyinen 1976, Divoky 1978). However, Arctic Terns do take crustaceans and insects more than do many other terns (Ashmole 1968, Pearson 1968). Consequently, there is some dietary overlap. We report here on the patterns of habitat (and food) use by Arctic Terns and Sabine's Gulls breeding in a mixed colony.

Our main objective was to determine if shared, possibly limiting, habitat and food resources were partitioned, and to describe how such partitioning was achieved. Although interspecific competition for limiting resources comes most readily to mind as a mechanism which promotes resource partitioning, it was not our aim to evaluate its role in this study. The issue is raised in speculation when results are discussed within the framework of three possible interpretations. We present indirect evidence which supports the competition interpretation with the intention of laying a foundation for further investigation into the patterns of habitat use within mixed colonies of Arctic Terns and Sabine's Gulls.

STUDY AREA AND METHODS

Arctic Terns and Sabine's Gulls have persisted in mixed colonies at East Bay, Southampton Island, N.W.T. (63°58′N, 81°50′W), since at least 1957 when they were first noted there by

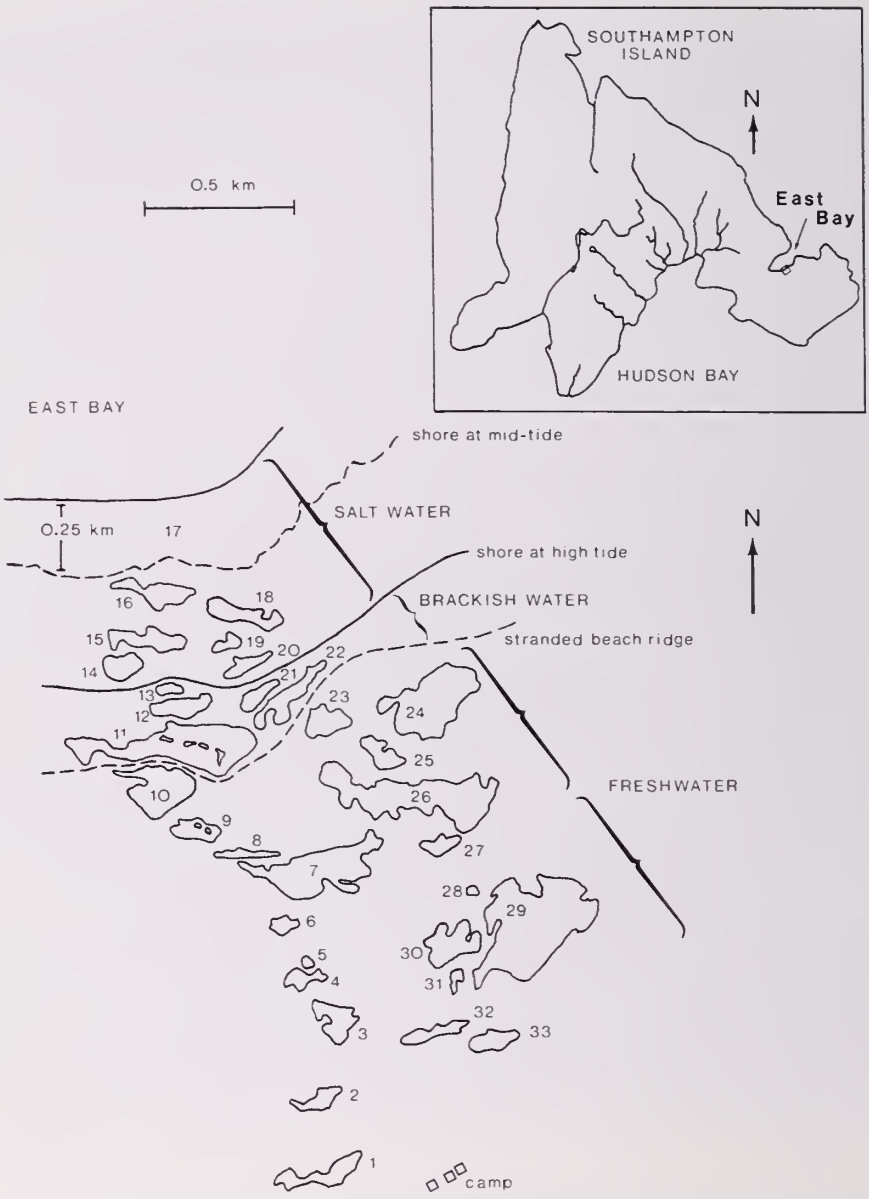

FIG. 1. Map of study area at East Bay, Southampton Island, N.W.T. (65°58′N, 81°50′W), showing numbered ponds and three macrohabitats.

T. W. Barry (pers. comm.). Both are abundant at East Bay, nesting together in varying concentrations along much of the south shore. Nesting is largely restricted to a narrow band of brackish water habitat just above the summer high tide line.

Our research was conducted on a 2.0 × 0.5-km study area located on the south shore of East Bay (Fig. 1), from 9 June to 14 August 1980. Thirty pairs of Sabine's Gulls and 42 pairs of Arctic Terns were nesting. A 4.5-km transect ran through the study area, incorporating 32 ponds, plus 0.25 km^2 of East Bay. The transect was established between 26 June and 5 July, as ponds became visible beneath the snow, covering 21 freshwater ponds, five brackish water ponds, and including the Bay, seven salt water "ponds."

Three aquatic macrohabitats were recognizable at East Bay: fresh-, brackish, and salt water (after Hoar 1975). Water salinities on the study area were measured in milli-osmols (mOsm) with an osmometer, and converted to parts per thousand (ppt) (Weast 1972–73). Ponds which registered between 0 and 5 ppt salinity were classified as freshwater; ponds measuring more than 5 ppt salinity and located above the summer high tide line were classed as brackish; water registering salinities greater than 30 ppt or located below the summer high tide line were considered salt water. The salt water macrohabitat at East Bay consisted of two distinct subunits: the intertidal region and the Bay itself. The intertidal region was characterized by numerous discrete basins which, by definition, were completely inundated by the waters of East Bay at high tide. These basins remained full when the tide receded, resulting in a series of salt water "ponds."

Within macrohabitats, four microhabitats were recognized: pond center (>1 m from shore), pond edge (≤1 m from shore), flooded tundra, and dry land (within 10 m of a transect pond). When sampling at the Bay, we used a 5-m boundary to distinguish edge from center, and "shore" was defined as the current tide line.

Sampling the Food Resource

The numbers, distribution (both among and within macrohabitats), and sizes of invertebrates (and vertebrates) in transect ponds were determined. Systematic water-column (sweep) sampling began 27 June and continued weekly until 8 August. We sampled each pond with a standardized sweep of 1 m^2 in surface area at both the center and edge using netting with 7.9 meshes/cm (after Bergman et al. 1977). We also took shallow benthic samples from transect ponds following the sweep sampling schedule. We used a squared-off coffee tin for benthic samples 5 cm wide, 10 cm long, and 1 cm deep.

Calculating biomass.—A selection of species-specific regression equations relating dry weight to length was made from the literature; these were used to calculate biomass (mg dry weight) from the number and average length (mm) of individuals in each prey group. A complete list of the equations used, including sources, and an explanation of their application is given in Abraham (1982).

Sampling Habitat Use by Gulls and Terns

The transect was walked at a slow and steady pace, once or twice per day, over all times of day. Complete coverage took approximately 3 h. Care was taken to keep a steady pace so the time spent at any one pond was the same from day to day.

The sampling technique used to quantify gull and tern foraging on the transect was a combination of instantaneous and ad libitum sampling (Altmann 1974). Instantaneous sampling records an individual's behavior at pre-determined moments (e.g., every 5 min for 2 h). In this study, each "pre-determined moment" began when the observer reached a pond on the transect and lasted until the pond was left behind—hence, the ad lib aspect of the method. A foraging attempt was defined as a strike of the bill at the feeding substrate.

The first foraging attempt by each bird at a pond was recorded, and the location (macro- and microhabitat) was noted. We also recorded the level of tides during each walk.

Supplemental observations of foraging gulls and terns were recorded as for transect observations. An observation was supplemental if it was made either: (1) off the transect at any time; or (2) on the transect, but not during a transect walk. Transect observations were used to analyse the use of macrohabitats by foraging gulls and terns; transect and supplemental observations were used for analysis of microhabitat use. When comparisons were made within macrohabitats, the bias of unequal effort introduced by the supplemental data was avoided.

Measuring Niche Segregation

The degree of ecological segregation (S_o) between two or more species (i.e., the probability that different resources are being used) can be quantified and expressed as the complement of niche overlap. Estimates of overlap (R_o) were calculated by Schoener's (1968) equation. R_o ranges from 0–1 inclusive. Thus, its complement S_o is $(1 - R_o)$.

RESULTS

The Food Resource

Specimens of potential prey collected in sweep and benthic samples from transect ponds represented eight taxa (Table 1). To detect changes in dry weight biomass (mg/m^2) among macrohabitats and over time for each of these groups, we divided the season into the stages of the birds' breeding cycle: pre-laying, egg (i.e., laying and incubation), chick-rearing, and post-fledging (Table 2). Because prey sampling started early in the egg stage, calculations of prey biomass were made using only the last three categories.

Midge larvae constituted the largest single contribution to the season's biomass in both fresh- (83.0%) and brackish water (92.6%) macrohabitats (Table 1). The salt water macrohabitat supported the greatest prey biomass of all macrohabitats, with amphipods providing virtually all of the total biomass (99.6%). Early in the egg stage, however, snow and ice on the salt water macrohabitat made prey inaccessible to foraging gulls and terns. Until the ice melted from East Bay (5–8 July), most foraging by both species was in the freshwater macrohabitat where prey was most accessible (Abraham 1982).

During the chick-rearing period, six Arctic Tern and 11 Sabine's Gull chicks were found dead. In addition to the stomach contents of these 17 individuals, regurgitations by four young and one adult Sabine's Gull were collected.

We analysed the diets of Arctic Tern and Sabine's Gull chicks on a presence-absence level. Of the six tern chick stomachs, amphipods occurred in two, single copepods in two, cranefly larvae in one, and cranefly adults in one. Additionally, six feedings of Arctic Tern chicks were ob-

TABLE 1

DRY WEIGHT BIOMASS (MG/M²) OF MAJOR POTENTIAL PREY TAXA[a] IN FRESH-, BRACKISH, AND SALT WATER MACROHABITATS

	Egg stage	Chick stage	Post-fledging stage
Freshwater			
Cranefly larvae[b]	27.2	13.5	12.5
Midge larvae[b]	199.4	132.6	203.0
Midge pupae	0.1	0.2	0
Water fleas	0.1	6.6	7.2
Fairy shrimp	2.2	11.3	28.8
Tadpole shrimp	0.1	0	0
Total	229.1	164.2	251.5
Brackish water			
Cranefly larvae[b]	0	10.4	0
Midge larvae[b]	576.0	278.1	121.1
Midge pupae	0	0.2	0.1
Water fleas	0.9	13.3	42.8
Fairy shrimp	0.1	5.3	2.7
Tadpole shrimp	0	0.1	0.1
Copepods	0	0.4	1.7
Total	577.0	307.8	168.5
Salt water			
Midge larvae[b]	9.7	7.9	0
Midge pupae	0	0.1	0
Copepods	0	0.4	0.1
Sculpin fry	0.2	1.2	0.4
Amphipods	5.8	6.2	0.1
Amphipods[b]	1636.5	540.9	2924.7
Total	1652.2	556.7	2925.3

[a] Craneflies (Tipulidae), midges (Chironomidae), water fleas (Daphinidae), fairy shrimp (Anostraca), tadpole shrimp (Notostraca), copepods (Calanoida and Cyclopoida), sculpin (Cottidae), and amphipods (Amphipoda).
[b] Benthic samples, all others sweeps.

served in which a total of four amphipods and two cranefly pupae (or larvae) were fed to chicks. Adult midges were the most common prey in samples from Sabine's Gulls, occurring in 14 of 16 samples. Cranefly adults occurred in eight samples, midge pupae in six, and egg shell fragments and downy feathers in four. One sample contained fish.

Habitat Use by Gulls and Terns

Observations made between 14 and 26 June (approximately the prelaying stage) could not be assigned to macrohabitats because snow cover

TABLE 2
FOUR STAGES IN THE BREEDING CYCLE OF ARCTIC TERNS AND SABINE'S GULLS

	Arctic Tern	Sabine's Gull
Pre-laying stage	12 June[a]–25 June (13 days)	12 June[a]–21 June (9 days)
Egg stage	26 June–16 July (20 days)	22 June–12July (20 days)
Chick stage	17 July–8 Aug. (22 days)	13 July–3 Aug. (21 days)
Post-fledging stage	9 Aug. –14 Aug.[b] (5 days)	4 Aug. –14 Aug.[b] (10 days)

[a] First day of fieldwork.
[b] Last day of fieldwork.

obscured these divisions. Alternatively, we made lists of the numbers and order in which foraging Arctic Terns and Sabine's Gulls were encountered during seven walks (made at all times of day) from the campsite to the sea ice. This "order of encounter" format lent itself to analysis by run tests (Sokal and Rohlf 1969:624). Of these seven runs, four were random ($P > 0.05$) and three were non-random ($P < 0.05$) (Abraham 1982). Twice Arctic Terns were concentrated near the sea ice and once Sabine's Gulls were concentrated there. Because over half of the runs were random and in light of the contrasting nature of the three non-random results, the macrohabitat distribution of Arctic Terns relative to that of Sabine's Gulls was probably random on the study area during the pre-laying stage.

In contrast, the macrohabitat distribution of Arctic Terns differed from that of Sabine's Gulls during the egg ($P < 0.001$), chick ($P < 0.001$), and post-fledging ($P < 0.005$) stages (Table 3); gulls were seen most often in the freshwater macrohabitat and terns in the salt water zone.

The observed patterns of habitat use by Arctic Terns and Sabine's Gulls were not influenced by tides. Tidal oscillations in the salt water macrohabitat were obscured by land-fast sea ice until approximately 6 July. Forty-one transect walks were made between 6 July and 13 August inclusive, covering 12 high tides, eight falling tides, nine low tides, and 12 rising tides. This frequency distribution did not differ from a uniform one ($\chi^2 = 1.24$, df = 3, $P > 0.05$). Additionally, the mean number of foraging observations per walk (i.e., foraging activity) did not differ among the four tidal stages for either Arctic Terns ($F_s = 0.42$, $P > 0.05$) or Sabine's Gulls ($F_s = 0.82$, $P > 0.05$).

Microhabitat use by Arctic Terns and Sabine's Gulls in the freshwater

TABLE 3

NUMBER OF ARCTIC TERNS (AT) AND SABINE'S GULLS (SG) OBSERVED FORAGING IN MACROHABITATS DURING THE EGG,[a] CHICK,[b] AND POST-FLEDGING[c] STAGES

		Macrohabitat		
		Freshwater	Brackish water	Salt water
Egg stage	SG	41	2	5
	AT	72	4	70
Chick stage	SG	105	9	13
	AT	91	10	168
		Freshwater	Salt water	
Post-fledging stage	SG	9	6	
	AT	1	14	

[a] $\chi^2 = 21.5$, df = 2, $P < 0.001$; m = 1.5 > $r/d^{1.5} = 0.71$: when expected values are small, χ^2 is valid if $r/d^{1.5} < m$, where r = the number of expected values <5, d = degrees of freedom, and m = smallest expected value (Lawal and Upton 1980:451).

[b] $\chi^2 = 95.1$, df = 2, $P < 0.001$.

[c] $\chi^2 = 9.6$, df = 1, $P < 0.005$.

macrohabitat was also different during the egg stage ($P < 0.001$) (Table 4). Sabine's Gulls foraged on dry land more often and over pond centers less often than expected, whereas Arctic Terns used pond centers more and dry land less than expected. Despite the inclusion of supplemental data, the egg-stage samples of both species in the brackish water macrohabitat and of Sabine's Gulls in the salt water macrohabitat were too small for species comparisons.

Because most flooded tundra disappeared from the study area by mid-July, comparison of microhabitat distributions during the chick stage was made using just dry land, pond edge, and pond-center categories. As in the egg stage, the freshwater microhabitat distributions of Arctic Terns and Sabine's Gulls during the chick stage were different ($P < 0.001$); Sabine's Gulls foraged over dry land, and Arctic Terns over pond centers and dry land (Table 4). As before, sample sizes in each non-freshwater macrohabitat were too small for species comparisons.

Niche Segregation

The degree of segregation of Arctic Tern and Sabine's Gull distributions over all macrohabitats (S_H) was calculated for each period. Macrohabitat segregation increased over time, from 38.6% in the egg stage to 48.9% during chick rearing to 60.0% post-fledging.

Microhabitat segregation (S_h) was calculated within time periods and macrohabitats where sample sizes allowed. These were then arcsin trans-

TABLE 4

NUMBER OF ARCTIC TERNS (AT) AND SABINE'S GULLS (SG) OBSERVED FORAGING IN FRESHWATER MICROHABITATS DURING THE EGG[a] AND CHICK[b] STAGES

		Microhabitat			
		Dry land	Flooded tundra	Pond edge	Pond center
Egg stage	SG	22	24	4	0
	AT	10	40	4	54
		Dry land	Pond edge	Pond center	
Chick stage	SG	129	11	7	
	AT	66	2	41	

[a] $\chi^2 = 47.4$, df = 3, $P < 0.001$, m = 2.6 > $r/d^{1.5} = 0.38$, see Table 3.
[b] $\chi^2 = 46.0$, df = 2, $P < 0.001$.

formed (Zar 1974:185) and averaged within each period. Average microhabitat segregation decreased over time from 40.5% in the egg stage to 33.2% during chick rearing.

Within each period, an estimate of total habitat segregation (S_T) was calculated across all macro- and microhabitat categories. Because of the complementary nature of the S_H and S_h trends, S_T values were relatively constant across the three periods: 69.4% in the egg stage, 64.3% during chick rearing, and 63.5% post-fledging.

DISCUSSION

Resource Partitioning

Pre-laying stage.—Sabine's Gulls and Arctic Terns arrived at East Bay when the tundra was still mostly snow-covered and the Bay frozen. Foraging opportunities were scarce for the first 6 days while less than 2% of the study area was open water (Abraham 1982). At that time, potential invertebrate prey included adult beetles (Coleoptera), springtails (Collembola), and "snow" spiders (Arachnida). Sabine's Gulls are known to prey heavily on "snow" spiders before melt (Sutton 1932, Bannerman 1962). In addition to invertebrates, seeds and other plant materials may provide an early food source for Sabine's Gulls (Sutton 1932).

At the onset of melt, both Sabine's Gulls and Arctic Terns were observed foraging in shallow melt pools throughout the study area. Potential prey included midge and cranefly larvae and adults, springtails, copepods, and the adults and larvae of aquatic and terrestrial beetles. During this pre-laying period, there was virtually no segregation of gulls and terns by macrohabitat. Widely scattered foraging opportunities and low prey avail-

ability encouraged individuals of both species to forage opportunistically, and to range over large areas in search of food.

Egg, chick, and post-fledging stages.—As the season progressed, the availability of foraging habitat (and prey) increased, and Arctic Terns and Sabine's Gulls showed different patterns of habitat (and food) use. Throughout the egg, chick, and post-fledging stages, macrohabitat segregation of Sabine's Gulls and Arctic Terns served to loosely partition total food resources; dipteran larvae and adults were available to Sabine's Gulls in the freshwater macrohabitat and amphipods to Arctic Terns in the salt water zone. These patterns of habitat and food use are similar to those published for other mixed colonies of Sabine's Gulls and Arctic Terns (McLaren et al. 1977) and for colonies of Arctic Terns (Parmelee and MacDonald 1960, Lemmetyinen 1976). However, fish usually form an important component of Arctic Tern diets. At East Bay, there was an apparent paucity of fish (Table 1), and Arctic Terns relied on amphipods and other aquatic invertebrates for feeding chicks. Sabine's Gulls preyed almost exclusively on insects; fish and large crustaceans were less well represented in the diets of Sabine's Gulls at East Bay than elsewhere (Gabrielson and Lincoln 1959, Divoky 1978, Blomqvist and Elander 1981). Microhabitat segregation facilitated further partitioning between gulls and terns within the shared freshwater macrohabitat; the adults and terrestrial larvae of dipterans were available to Sabine's Gulls on dry land, and fairy shrimp, water fleas, and emerging adult dipterans to Arctic Terns in pond centers.

Interpretation

Why do Arctic Terns and Sabine's Gulls at East Bay prefer the habitats (and foods) they do? We offer three interpretations of the observed patterns: (1) coincidence, (2) optimal foraging, and (3) interspecific competition. Suppose the patterns of resource partitioning by these larids were purely coincidental, i.e., evolved in each species independently. If so, the degree and nature of macro- and microhabitat segregation of the two species would be due to chance. At East Bay, macro- and microhabitat segregations were complementary. That is, similarity along one dimension coincided with dissimilarity along the other, and resulted in a relatively constant level of spatial segregation. Interspecific differences "regulated" by chance, not natural selection, would probably be less systematic.

An alternate interpretation of the observed patterns of habitat and food use is optimal foraging, i.e., each species pursued the prey it was best suited to hunt. Patterns of habitat use by gulls and terns could then be explained in terms of the habitats used by their prey. This interpretation is satisfactory for Arctic Terns because they are behavioral specialists

when foraging and their concentration in the salt water zone probably has an anatomical/behavioral basis. Because terns do not regurgitate undigested foods (Tinbergen 1961), they are limited to carrying one prey item per feeding trip. Thus, when feeding chicks, the pursuit of large prey is likely the most economical strategy (Schoener 1971). Amphipods, measuring up to 25 mm in length, were the largest prey in samples at East Bay and were found in the salt water macrohabitat. The only time terns regularly used the freshwater macrohabitat, where prey were small, was before hatch; some continued to forage there even after the salt water zone became free of snow and ice (Abraham 1982). Sabine's Gulls, on the other hand, can (and do, especially at other colonies) efficiently use both small and large prey items throughout the season because they feed their chicks by regurgitation (Brown et al. 1967). At East Bay, most amphipods (96%) were found in shallow benthic samples at the edges of salt water "ponds" and were as accessible to Sabine's Gulls as freshwater dipteran larvae. Yet, during the egg and chick stages, Sabine's Gulls did not exploit the salt water macrohabitat despite the greater prey biomass available. As a third alternative, we suggest that Sabine's Gulls were excluded from the salt water zone because of the abundance and competitive abilities of Arctic Terns there. Below, we present evidence to support this interpretation.

Partitioning of habitat and food resources by East Bay Arctic Terns and Sabine's Gulls occurred during the 1980 breeding season. However, the mere presence of niche differences among coexisting species, i.e., "first-level" (Huey 1979) evidence for competition, is inconclusive (Schoener 1974, Huey 1979, Nudds 1982). Therefore, we considered "second-level" evidence, such as niche complementarity (Rosenzweig and Winakur 1969, Schoener 1974) necessary before invoking interspecific competition as a possible factor in the origin and/or maintenance of resource partitioning by East Bay Arctic Terns and Sabine's Gulls. Second-level evidence from this study supports the interpretation that interspecific competition may have influenced the evolution of the observed niche differences: macro- and microhabitat segregations were complementary. Such systematic changes in the segregation of species along complementary dimensions represent one of three predicted patterns of niche "over-dispersion" that Schoener (1974) suggested result from interspecific competition (see also Rosenzweig and Winakur 1969).

To further examine this interpretation, natural and/or manipulative experiments are needed. Ideally, the patterns of foraging habitat (and food) use by Arctic Terns and Sabine's Gulls breeding in single-species colonies should be quantified and compared to those in mixed colonies. Such an approach could generate a third level of evidence for a competition hypothesis.

SUMMARY

The patterns of habitat use by foraging Arctic Terns (*Sterna paradisaea*) and Sabine's Gulls (*Xema sabini*) were quantified and compared at East Bay, Southampton Island, N.W.T., during the 1980 breeding season.

Segregation of gulls and terns at the macrohabitat level served to loosely partition total food resources; dipteran larvae and adults were available to Sabine's Gulls in the freshwater macrohabitat and amphipods to Arctic Terns in the salt water zone. Microhabitat segregation resulted in further partitioning, especially when macrohabitat segregation was lowest (i.e., during egg-laying and incubation). Three explanations for these patterns are discussed: coincidence, optimal foraging, and interspecific competition. Arguments in support of both optimal foraging and competition interpretations are offered to best account for the habitat preferences of Arctic Terns and Sabine's Gulls at East Bay.

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COMPARATIVE FORAGING ECOLOGY OF LOUISIANA AND NORTHERN WATERTHRUSHES

ROBERT J. CRAIG

Closely related and ecologically similar species have been the focus of many recent studies on the behavior and ecology of birds. Such studies have investigated the possibility of interspecific competition and conditions that might act to reduce competition (MacArthur 1972, Cody 1974). Conditions considered include differences in foraging zones and methods (MacArthur 1958; Morse 1967, 1971), microhabitat selection (Wiens 1969), interspecific territoriality (Miller 1968, Rice 1978), character displacement (Abbott et al. 1977), contiguous allopatry (Diamond 1970, Terborgh and Weske 1975), and preferences for size and type of food (Hespenheide 1975).

Wiens (1977) pointed out that the mere existence of interspecific differences may not adequately explain the ability of species to coexist, because the differences could have evolved in response to selective forces other than competition. Furthermore, interspecific competition may not be selectively important in variable environments, where populations are often below equilibrium densities. The use of measures of niche overlap to assess the intensity of competition has also been criticized in situations of unlimited resources (e.g., Pianka 1976, Abrams 1980).

However, in a review of studies of competition, Schoener (1982) noted that even in variable environments periods of limited resources may often occur. Species demonstrated to have high niche overlap and low amounts of competition may even verify the importance of interspecific competition. He hypothesized that similar species converge in using superabundant resources, for which competition would be unnecessary, and diverge in using limited resources, for which competition would be great.

I have studied sympatric populations of the ecologically and morphologically similar Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes to determine whether their feeding behavior and prey availability in their territories indicate the occurrence of interspecific competition. Foraging of other wood warblers (Parulinae) has been studied extensively by MacArthur (1958), Rabenold (1978), and Morse (1980), but except for the Ovenbird (*S. aurocapillus*; Zach and Falls 1978), studies of *Seiurus* spp. have been largely qualitative (Bent 1953; Eaton 1957, 1958). Bent (1953) and Eaton (1957, 1958) reported that the insectivorous waterthrushes, though primarily terrestrial and as-

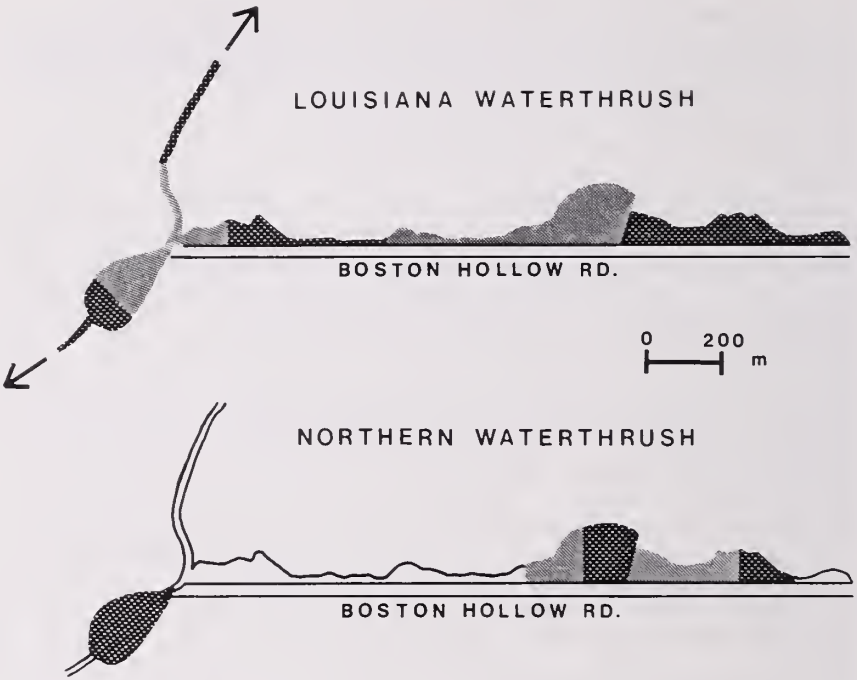

FIG. 1. Distribution of waterthrush territories at Boston Hollow, 1980. Width of swamp equals scale × 2; dark and light stipple patterns denote shapes of adjacent territories.

sociated with wetlands, can feed in leaf litter, water, foliage, and on flying insects.

STUDY AREAS AND METHODS

Habitats.—I studied adult waterthrushes in northeastern Connecticut from early April to mid-August, 1978–1980. Despite Bent's (1953) report that the species only rarely share the same site, my 9 years of observations in Connecticut indicate that they regularly breed near each other.

My principal study site, Boston Hollow, was located in Yale Forest, Ashford, Tolland Co. The area includes a small, alternately rushing and swampy stream that runs between the steep bedrock walls of a ravine. At the ravine's south end a similar stream joins the outflow, and the combined streams flow into a series of swamps (Fig. 1).

The brook portions of the habitat contain mesic, mature deciduous forest dominated by yellow birch (*Betula lutea*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and an open understory of spicebush (*Lindera benzoin*) and black alder (*Ilex verticillata*). Swampy portions have a generally young canopy of hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), yellow birch, and red maple, and a dense understory of black alder, speckled alder (*Alnus rugosa*), and sweet pepperbush (*Clethra alnifolia*). The swamp at the south end of Boston Hollow is mainly deciduous, with a canopy largely composed of red maple.

I made limited observations at about 25 other sites throughout New England in addition to Boston Hollow. Observations from these sites were used to assess the generality of my findings at Boston Hollow.

Territoriality and banding.—I located territorial boundaries by recording the locations of song perches and territorial interactions. Territory size was determined with compass and tape measure. Additionally, I color banded adults for individual recognition, and weighed birds with a Pesola spring balance to ±0.1 g.

Foraging behavior.—In observing foraging, I noted the type of habitat used, the method of foraging, and the number of foraging activities. Based on Eaton's (1957, 1958) findings and my preliminary examinations, I divided waterthrush foraging sites into four categories: (1) water, (2) ground, (3) foliage, and (4) air. I separated each year's data into those collected before and after the leafing out of trees (about 10 May) because my preliminary observations indicated that habitat preference changed after leaf emergence in spring.

My observations also indicated that four general foraging methods occur: (1) picking, (2) leaf-pulling, (3) hawking, and (4) hovering. Of these, only leaf-pulling is uncommon among wood warblers (Bent 1953). It involves pulling dead leaves from litter or water with the bill and inspecting the revealed substrate or underside of the leaves for prey. For analysis of data on foraging methods, I again separated my observations into those collected before and after leaf emergence.

Invertebrate sampling.—I found that aquatic invertebrates predominated in the diet of waterthrushes, so I assessed prey availability only in the aquatic environment. During the study I sampled at eight different territories per species. Of these, two of the territories of Louisiana Waterthrushes overlapped with two of Northern Waterthrushes, but only 8% of the samples were from the zone of overlap.

I sampled each territory three times over the breeding season: (1) during incubation (mid-May), (2) during feeding of nestlings (early June), and (3) during feeding of fledglings (late June). Moreover, in 1980 I also sampled in late April to assess invertebrate biomass at the start of the breeding season.

Dip netting was used to sample because the technique caught benthic and swimming organisms, both of which waterthrushes eat. Although this method may have underestimated the number of fast-moving invertebrates, the results appeared to agree well with my visual estimates of the relative abundance of aquatic taxa. To sample I divided each territory into 10 "blocks" and then randomly selected a spot in each block. At each spot I submerged the net (9.5 × 7.5 cm; 16 meshes/cm) and moved it back and forth over 0.5 m for 10 sec. I then hand sorted samples, measured and identified specimens, stored specimens in 70% ethanol, and determined standardized wet weights (Craig 1981) of each sample.

I also established 11 size categories of prey, all but the first with a range of 3 mm (Table 1). The first, ≤4 mm, was mainly comprised of organisms nearly 4 mm in length, because organisms shorter than 3 mm could not be successfully removed from the samples. Organisms >19–22 mm were rare and consequently deleted from further analysis.

It was necessary to take many invertebrate samples because aquatic invertebrates are not distributed randomly (Southwood 1966). Because field time was divided between processing samples and observing bird behavior, insufficient time was available for sampling invertebrates in other habitats. However, the objective in studying prey was to compare the food of the two waterthrushes rather than to determine the absolute abundance of prey. If prey biomasses differ between the territories of the species, which are both closely associated with wetlands, I felt that such differences would most likely occur in the aquatic environment.

To determine whether the taxa in my invertebrate samples were the same as those actually taken by waterthrushes, whenever possible I recorded the type of prey the birds ate. Such data are incomplete, however, because it was often difficult to identify small prey.

TABLE 1

SIZE DISTRIBUTION OF INVERTEBRATE SAMPLES FROM WATERTHRUSH TERRITORIES

Species	Size class (mm)[a]						
	4	4–7	7–10	10–13	13–16	16–19	19–22
S. motacilla							
$\bar{x}$[b]	7.0	137.4	66.4	22.5	7.4	1.6	1.1
	±5.2	±62.1	±31.7	±6.9	±3.5	±1.3	±1.1
S. noveboracensis							
$\bar{x}$	5.1	150.4	77.8	24.6	2.1	<1	<1
	±4.3	±65.5	±70.0	±22.8	±1.6		

[a] Only those classes represented in most territories are included.
[b] Mean (±SD) number of individuals/sample, all three sampling dates combined.

Analysis.—To determine the overlap in feeding behavior between species I used the equation:

$$\text{Overlap} = 1 - 0.5 \Sigma |p_{x_i} - p_{y_i}|,$$

where p_x and p_y are the frequencies of resource use of species x and y, respectively, in category i (Schoener 1970). Abrams (1980) recommended this index because of its ease of computation and lack of a number of underlying assumptions.

RESULTS

Territoriality.—Territories of Louisiana Waterthrushes ($\bar{x}$ = 0.67 ha, SD = ±0.35, N = 9), and Northern Waterthrushes ($\bar{x}$ = 0.47 ha, SD = ± 0.26, N = 10) were not significantly different in size (Fig. 1). Of 27 waterthrush territories studied in Boston Hollow, 17 were overlapping. *Seiurus motacilla* territories overlapped from 73–100% of adjacent territories of *S. noveboracensis.* However, despite the overlap and occasional feeding of the species within a few meters of each other, they did not exhibit interspecific territoriality or appear to aggressively interact. In Cornwall, Connecticut, both species even built nests in the same upturned root (M. Root, pers. comm.). In contrast, both species were intensely aggressive toward conspecifics.

Weight.—Of 52 waterthrushes banded during this study, 14 *motacilla* and 19 *noveboracensis* were resident adults with comparable weights. I found little sexual difference in weight, but I did find that *motacilla* ($\bar{x}$ = 20.4 g, SD = ± 0.88) was significantly heavier (t = 16.6, df = 31, P < 0.01) than *noveboracensis* ($\bar{x}$ = 16.1 g, SD = ± 0.62).

Foraging.—When searching for prey, the two species exhibited similar behaviors. In aquatic foraging, birds typically alternated between wading and walking along logs, on branches, and at the water's edge, and they

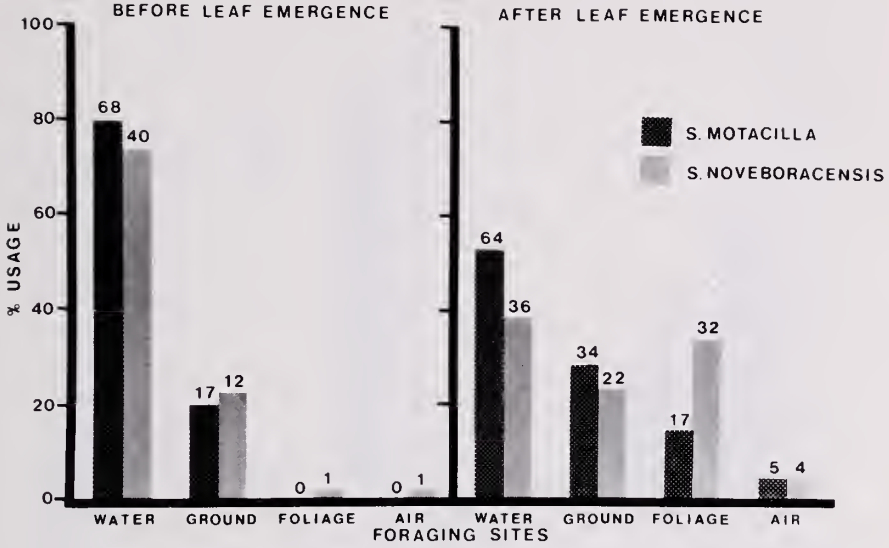

FIG. 2. Use of foraging sites, based on data from 1978–1980. Numbers above bars represent total observations.

fed on both submerged and floating organisms. On a few occasions I watched birds flutter over the water to capture prey from its surface. Ground feeding included capturing prey on mud, in leaf litter, on rocks, and on moss. When feeding on woody plants, the birds walked on stout branches and picked prey from the foliage and stems with movements similar to those used for catching terrestrial prey.

Because picking did not occur in the air, hawking occurred only in the air, and leaf-pulling occurred only on the ground and in water, results for foraging methods mirror those of foraging sites to some extent. However, the categories involved in the two data sets are sufficiently distinct to warrant separate analysis. The two predominant foraging methods, picking and leaf-pulling, were used in both major foraging sites, the water and ground.

Comparison of pooled data on feeding sites revealed that both species made significant changes in their foraging sites after leafing out (*motacilla*: $\chi^2 = 22.4$, df = 2, N = 205, $P < 0.01$; *noveboracensis*: $\chi^2 = 24.6$, df = 2, N = 148, $P < 0.01$). Cumulative Chi-squares computed from individual year's data yielded similar results. The waterthrushes overwhelmingly fed in water early in spring, but although water remained an important feeding habitat, they also used other sites after leaf emergence (Fig. 2).

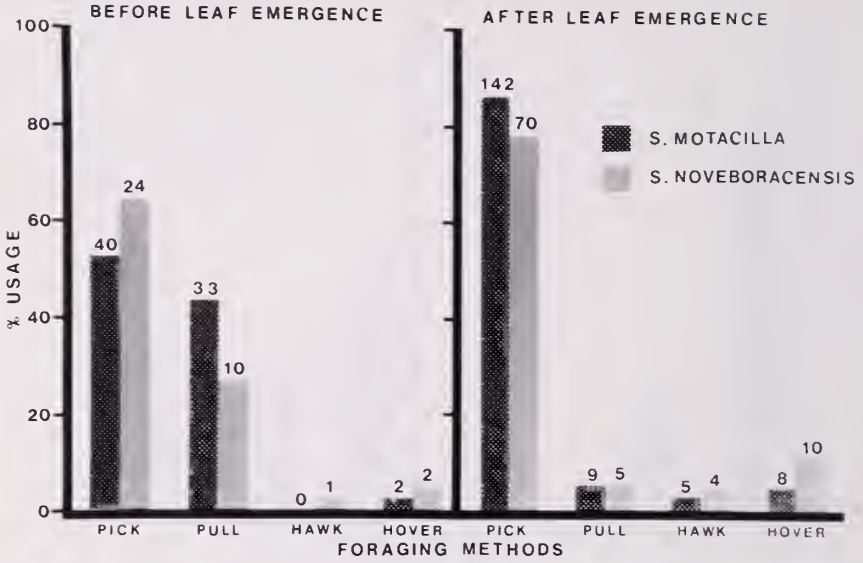

FIG. 3. Use of foraging methods, based on data from 1978–1980. Numbers above bars represent total observations.

Pooled data also revealed that the two species foraged similarly prior to leafing out ($\chi^2 = 3.3$, df = 2, N = 139, $P > 0.05$), but diverged significantly afterwards ($\chi^2 = 12.1$, df = 3, N = 214, $P < 0.01$). Again, cumulative Chi-squares corroborate these findings. Northern Waterthrushes seemingly had a wider foraging range, using foliage, ground, and aquatic sites, whereas the Louisiana Waterthrushes used mostly ground and aquatic sites.

My comparison of pooled data on foraging methods revealed a change in behavior of the two species after leafing out (*motacilla*: $\chi^2 = 53.8$, df = 3, N = 239, $P < 0.01$; *noveboracensis*: $\chi^2 = 11.9$, df = 3, N = 126, $P < 0.01$), and cumulative Chi-squares were again in agreement. Before leafing out, both species used picking and leaf-pulling commonly, but afterwards picking clearly predominated. The frequency of leaf-pulling dropped sharply, and aerial foraging increased slightly for both species (Fig. 3). In contrast, analyses of pooled and annual data showed that the species did not significantly differ from each other in foraging methods (before leafing out: pooled $\chi^2 = 4.1$, df = 2, N = 112, $P > 0.05$; after leafing out: pooled $\chi^2 = 4.1$, df = 3, N = 253, $P > 0.05$).

The similarity between the species in their feeding behavior was reflected in overlap calculations. For the pooled data, use of foraging sites

TABLE 2
TAXONOMIC COMPOSITION OF INVERTEBRATE SAMPLES FROM TERRITORIES OF WATERTHRUSHES

Taxon[a]	*S. motacilla*[b]	*S. noveboracensis*
Trichoptera	39.8 ± 29.7	9.4 ± 9.9
Ephemeroptera	40.0 ± 32.0	40.3 ± 46.6
Megaloptera	6.1 ± 6.9	5.1 ± 3.9
Diptera		
Miscellaneous	7.4 ± 5.4	14.4 ± 17.0
Chironomidae	103.4 ± 53.0	104.6 ± 98.6
Coleoptera		
Dytiscidae adult	4.4 ± 2.1	6.5 ± 5.1
Dytiscidae larvae	7.6 ± 6.5	10.8 ± 6.4
Helodidae	5.8 ± 11.0	5.9 ± 5.7
Isopoda	18.6 ± 11.7	16.3 ± 8.2
Oligochaeta	3.5 ± 2.3	5.9 ± 7.3
Gastropoda	2.3 ± 3.4	43.0 ± 34.8

[a] Only those taxa represented in most territories are included.
[b] Mean number of individuals/sample (±SD), all three sampling dates combined.

exhibited an overlap of 0.98 before and 0.92 after leaf emergence. For foraging methods the equivalent values were 0.83 before and 0.92 after leaf emergence.

Prey taken.—During my observations I could identify some types of prey captured by waterthrushes, particularly for *motacilla*. Because *motacilla* sometimes fed in more open sites, it was easier to observe than *noveboracensis*. Also, *motacilla* may take larger and therefore more easily identifiable prey, as discussed below. I saw *motacilla* eat the following types of aquatic organisms: isopods, gastropods, nymphs of Ephemeroptera, larvae of Trichoptera, larvae of Culicidae, and larvae of Dytiscidae. In addition, I observed birds feeding on terrestrial chilopods, lepidopteran larvae, adults of Culicidae, and unidentified emergent aquatic insects. *S. motacilla* ate organisms up to about 3 cm in length (centipede), and I saw individuals removing larvae of Trichoptera from their cases.

I could identify few prey taken by Northern Waterthrushes. Adults of Culicidae were eaten, and in late May both *noveboracensis* and *motacilla* ate caterpillars which were then emerging abundantly. These caterpillars were also fed to young. The largest item seen eaten by *noveboracensis* was about 1 cm long.

By turning wet leaves at waterthrush feeding sites in a manner analagous

TABLE 3
BIOMASS OF INVERTEBRATES FROM SAMPLES IN WATERTHRUSH TERRITORIES

Species	Sampling date		
	Mid-May[a]	Early June	Late June
S. motacilla	0.84 ± 0.64	0.77 ± 0.23	0.62 ± 0.52
S. noveboracensis	1.08 ± 0.51	0.53 ± 0.48	0.46 ± 0.19

[a] Mean (±SD) weight/sample (g).

to that used by waterthrushes, I found ready access to ephemeropteran nymphs and chironomid larvae. These observations, as well as my findings above, agree with Eaton's (1957, 1958) reports on types of aquatic prey eaten by waterthrushes.

Prey available.—Among 18 major invertebrate taxa found in my aquatic samples, Ephemeroptera and Chironomidae were most numerous (Table 2). There were significantly more Trichoptera ($t = 3.9$, df = 14, $P < 0.01$) and fewer Gastropoda ($t = 2.9$, df = 14, $P < 0.05$; log-transformed data) in *motacilla* than in *noveboracensis* territories.

By comparing percentiles, I found that territories of waterthrushes differed in only the upper 2% of their invertebrate size distributions ($t = 2.6$, df = 14, $P > 0.05$; log-transformed data). Thus, invertebrates >13 mm occurred more frequently in territories of *motacilla* than in those of *noveboracensis*. Furthermore, territories of *motacilla* averaged 15% more than *noveboracensis* in biomass of invertebrates >13 mm. The Trichoptera comprised 52% of the individuals >13 mm in *motacilla* territories, which is 21% more than in *noveboracensis* territories.

No statistical differences between territories of the two waterthrushes ($F = 0.2$, df = 1, N = 2, $P > 0.05$; ANOVA) are reflected in analysis of invertebrate biomass (Table 3). I also detected no difference between the individual territories of each species ($F = 1.5$, df = 12, N =16, $P > 0.05$; ANOVA). However, I did find a difference among the biomasses recorded on the three sampling dates ($F = 4.7$, df = 2, N = 3, $P < 0.05$; ANOVA). Biomass was highest early in the season (Duncan's test) and declined afterwards. The decline appeared steepest in territories of Northern Waterthrushes. A summer decline in invertebrate biomass is typical for small streams in the region (R. Pupedis, K. Thompson, pers. comm.), but an additional comparison of samples collected in late April, 1980 with early May samples did not differ ($t = 0.76$, df = 14, $P > 0.05$).

DISCUSSION

The two waterthrushes have usually been treated as ecologically distinct species, with *motacilla* associated with streams in deciduous woodland

and *noveboracensis* with swamps in coniferous forest (Bent 1953; Eaton 1957, 1958). Although these habitat preferences are generally true, my study clearly demonstrates that the waterthrushes can overlap in several respects.

Foraging of the two waterthrushes is similar, apparently overlapping to a greater degree than is the case in other closely related species (e.g., Schoener 1970, Voigts 1973). The similarity of habitat use in these species before leafing out may reflect the relatively high biomass of aquatic prey in that season. Differences after leafing out might be attributed to increased competition for a declining supply of aquatic prey, thus necessitating movement into alternate environments. This explanation, however, does not account for the remaining high overlap between the species.

Another explanation not dependent upon accounting for high overlap and lack of aggression between the species can be offered. Perhaps in the Pleistocene, separation of populations of an ancestral waterthrush occurred, such as is described for other Parulinae by Mengel (1964). These isolates might have evolved different behavioral traits facilitating foraging in different habitats. Divergence detected today might be a by-product of independent specialization of each species rather than a result of interspecific competition.

My data on foraging methods also demonstrate high overlap between the two species. The lack of significant differences suggests that differences in foraging do not serve to reduce competition between the two species. Thus, interspecific territoriality, divergence in foraging sites, and divergence in foraging methods do not appear to be involved in ecologically separating waterthrushes.

Invertebrate data do suggest that waterthrushes select breeding habitats with aquatic organisms of different size distributions. Larger insectivorous birds are known to eat larger prey than smaller but similarly feeding birds (Hespenheide 1973). However, it is not known if selection by *motacilla* of territories which contain an average of 15% more large organisms than in *noveboracensis* territories reduces competition between the two species.

I conclude that evidence for competition between the Louisiana and Northern waterthrushes is weak, despite their apparent similarity. This suggests that competition is not always a factor influencing use of resources by ecologically similar species. Rabenold (1978) suggested that, in the northeast, foliage invertebrates undergo a summer pulse in abundance so great that they are not in limited supply for predators. If this also occurs in prey consumed by waterthrushes, then competition need not occur, and foraging behavior of the species need not diverge. In addition, other as yet undetermined factors, such as those that might act to reduce waterthrush populations below equilibrium densities, may also be responsible for reducing the intensity of competition between these species.

SUMMARY

The territoriality, foraging behavior, and aquatic prey of breeding Louisiana (*Seiurus motacilla*) and Northern (*S. novaboracensis*) waterthrushes were studied in northeastern Connecticut. Although intensely aggressive toward conspecifics, the species had overlapping territories and were similar in both use of foraging sites and in methods of foraging. Few significant differences between territories of the two species occurred with respect to biomass, taxonomic composition, and size distribution of aquatic invertebrates. Despite similarity in behavior and in resource availability of their territories, evidence for interspecific competition between the species appeared weak. It is suggested that the waterthrushes coexist without competing because resources are not in limited supply, and that differences which do exist between the species have evolved in response to factors other than competition.

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METABOLISM AND FOOD SELECTION OF EASTERN HOUSE FINCHES

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The establishment and dispersal of introduced species of birds is best documented by the many studies of the House Sparrow (*Passer domesticus*) (Johnston 1964, 1973; Hudson and Kimzey 1966; Selander and Johnston 1967; Johnston and Selander 1971, 1973; Johnston et al. 1972; Blem 1973, 1974, 1975), and the Eurasian Starling (*Sturnus vulgaris*) (Kessel 1953, 1957; Blem 1981). However, with very few exceptions (Lack 1949, Calhoun 1947), most of this research did not occur until many years after the populations were first established. The recent introduction of the House Finch (*Carpodacus mexicanus*) into the eastern half of the United States (Elliott and Arbib 1953, Aldrich and Weske 1978) and dispersal into Virginia (Blem and Mehner 1981) provided us the opportunity to examine avian adaptation to a new environmental regime as it occurred and not after the fact. The present study: (1) documents the metabolic response of Virginia House Finches to ambient temperature, photoperiod, and food composition; and (2) quantifies the poor tolerance of Virginia House Finches of low temperatures. The dependence of these birds on artificial food sources for survival may be a possible ecological basis for significant morphological differences, particularly increased bill size, which have arisen between the eastern race and the parental stock (Aldrich and Weske 1978, Aldrich 1982).

METHODS

All birds used in this study were trapped at feeders near Richmond, Virginia, in December 1980, or January 1982. They were kept in flight cages for several days at room temperature (25°C ± 2) and at a photoperiod of 12L:12D. All birds initially were given water and chick starter mash ad lib. In preparation for each metabolic test, birds were placed individually in small cages of hardware cloth (Martin 1967) and acclimated to the test temperature for at least 3 days. Each bird was weighed at the beginning of each test and given a known amount of test food, varying from 10–50 g depending on ambient temperature. Water was provided ad lib. All experiments were run in constant temperature cabinets where temperature was controlled to ±1°C; relative humidity did not exceed 50%. After 2 days, each bird was reweighed and the excreta and remaining food were collected, oven-dried, and weighed. The heat of combustion of food and feces was determined by bomb calorimetry. Gross energy intake (kJ of food consumed) and excretory energy (kJ of feces and urine) were calculated from appropriate weights and heats of combustion (see Kendeigh 1967, Kendeigh et al. 1977). Metabolized energy (gross energy intake minus excretory energy) and efficiency of utilization (metabolized energy/gross energy intake ×100) were computed for all measurements. Tests generally were run at 2, 7, 14, 20, 26, and 32°C and photoperiods of 12L:

TABLE 1

COMPOSITION OF FOODS USED IN METABOLIC STUDIES AND PREFERENCE TESTS OF HOUSE FINCHES

Food	kJ/g	Lipid (%)	Protein (%)	Ash (%)	Carbohydrate (%)
Chick mash	17.2	6.6	19.0	10.5	63.9
Chick mash + oil	20.5	25.3	15.0	8.4	51.3
Chick mash + soy	18.0	3.6	31.0	8.4	57.0
Milo	18.0	3.1	10.0	1.9	85.0
Millet	18.4	3.6	11.3	5.7	79.4
Sunflower	28.5	40.7	42.1	2.3	14.9

12D and 10L:14D with each of three different foods. The single exception was elimination of 2°C tests with protein-supplemented food; poor survival of birds tested at 7°C indicated that 2°C tests were impossible. Every test, including each combination of photoperiod, temperature, and food type, involved three replicates performed with each of four birds, except those tests in which birds died, whereupon the test was completed with the remaining birds. Fifteen different House Finches were used. The food types used were chick starter mash, fat-supplemented mash consisting of chick mash plus 20% (by weight) vegetable oil (shortening), and protein-supplemented mash composed of chick mash containing 50% ground soy meal. The percentage of protein in each food type was obtained by Kjeldahl analysis, lipids by Soxhlet extraction in 5:1 petroleum ether:chloroform, ash by combustion in a muffle furnace at 550°C, and carbohydrate by subtraction (Table 1). For comparative purposes, House Sparrows were tested in the same fashion as House Finches at temperatures of 7 and 14°C, and a photoperiod of 12L:12D, using all three foods. Nine different sparrows were used and two replicates were made for each bird at each combination of conditions.

Food preference tests.—In preparation for each food preference test, birds were placed individually in the cages used for the metabolic tests, and given water and one of the three test foods ad lib. They were acclimated to test conditions for at least 3 days. At the beginning of each test, birds were presented with 10 g of each of the three types of mash in separate containers. The position of the food containers was systematically changed with each replicate to eliminate bias. Three replicates were completed with each bird. The amount of each food eaten was presumed to be the difference between weights of food at start and finish of each test. Test periods lasted 3 h. Control tests indicated that there was no weight change of foods under these conditions. This procedure was repeated on three different days to complete a given test. Four different tests were run, all on a photoperiod of 12L:12D, at temperatures of 7, 14, 20, and 26°C, using five different finches. The same procedure was repeated, using milo, white millet, and sunflower seed as the test foods. The composition of the seeds was determined as described for plain and supplemented chick mash above, and is listed in Table 1. Seed preference tests were run on a photoperiod of 12L:12D, at temperatures of 7, 14, and 20°C using four different finches with three replicates of each bird.

All analyses were performed by means of the Statistical Analysis System (SAS Institute 1982). A significance level of $P < 0.01$ was used in all tests. Covariance analyses of body weight and metabolism were computed with photoperiod, food, and sex included as clas-

TABLE 2
ANALYSIS OF COVARIANCE OF HOUSE FINCH BODY WEIGHT (G)

Source	df	Sum of squares	*F*
Model	10	68.5	3.02**
Error	108	244.9	
Total	118	313.5	
Sex	1	27.99	12.34**
Photoperiod	1	0.55	0.24
Food type	2	19.29	4.25**
Temperature	6	15.57	1.14

** $P \leq 0.01$.

sification variables (see Zar 1974), and weight, weight change, and ambient temperature included as covariants.

RESULTS

Body weight.—Covariance analysis indicates that sex and food type have significant effects on mean body weight during measurements of metabolism (Table 2). House Finches were able to maintain body weights at low ambient temperatures (i.e., below 20°C) only while being fed oil-supplemented mash (see Table 3), and mean body weight was significantly higher on this diet than on others ($t = 3.2$). Weight of the birds was lowest while being fed the unsupplemented mash and weight loss became more severe as ambient temperature decreased. At 2°C, 12L:12D, three of four birds being tested died. Weight losses of birds being fed soy-supplemented mash were minor until ambient temperatures of 7°C, when weight loss became severe and three of four birds being tested died, two on a photoperiod of 12L:12D and one at 10L:14D. An additional bird was removed from the 10L:14D photoperiod test due to extreme weight loss. The remaining birds were not tested at 2°C on the soy-supplemented mash; we assume they would not have survived. All deaths were preceded by large weight losses. The mean weight of six birds that died during the experiments was 16.1 g. The mean weight of 15 living birds (computed throughout all experiments, N = 282) was 20.0 ± 0.2 g (SE). Males (21.7 ± 0.2 g; N = 92) weighed more than females (20.6 ± 0.1; N = 190), and the difference is significant ($t = 4.9$). House Sparrows tested as "controls" maintained body weight under all conditions, but weighed significantly more ($t = 3.3$) when fed the oil-supplemented food.

Analysis of covariance indicates that differences in metabolized energy due to sex and photoperiod were not statistically significant; those data

TABLE 3

BODY WEIGHT, METABOLIZED ENERGY, AND EFFICIENCY OF USE IN HOUSE FINCHES

Temperature (°C)	N	Body weight[a] (g)	Metabolized energy[a] (kJ/day)	Efficiency[a] (%)
		Mash		
2	2	19.3 ± 2.5	65.5 ± 2.3	69.2 ± 0.6
7	8	20.0 ± 0.4	58.8 ± 3.1	71.3 ± 1.0
14	8	21.0 ± 0.4	44.2 ± 2.7	69.8 ± 1.1
20	8	20.8 ± 0.6	47.7 ± 1.9	73.2 ± 1.0
26	8	20.5 ± 0.5	37.4 ± 1.5	72.9 ± 0.8
32	4	20.7 ± 0.5	43.4 ± 3.1	72.6 ± 1.5
35	4	20.0 ± 0.3	38.1 ± 2.0	76.6 ± 0.4
		Soy-supplemented mash		
7	4	19.8 ± 0.6	41.8 ± 2.4	61.9 ± 2.3
14	4	20.3 ± 0.5	54.5 ± 2.2	62.3 ± 1.3
20	6	21.4 ± 0.5	50.8 ± 2.2	63.8 ± 1.8
26	8	21.6 ± 0.8	39.2 ± 3.2	61.1 ± 2.1
32	6	21.5 ± 0.8	47.1 ± 3.5	66.8 ± 1.5
		Oil-supplemented mash		
2	4	21.6 ± 0.7	91.0 ± 8.0	65.9 ± 1.8
7	4	21.5 ± 0.6	87.6 ± 2.6	74.8 ± 2.8
14	4	21.8 ± 0.3	74.3 ± 5.2	77.9 ± 1.3
20	6	21.7 ± 0.6	65.4 ± 5.5	74.3 ± 1.7
26	8	21.7 ± 0.6	52.5 ± 3.2	81.7 ± 0.8
32	6	21.7 ± 0.7	57.3 ± 4.4	79.3 ± 2.8

[a] Values are means ± 1 SE.

were pooled and reanalyzed using food as a class, and weight, weight change, and temperature as covariants. Metabolized energy is most affected by temperature, followed by food type, weight change, and weight, in that order, as judged by the portion of the total sum of squares attributable to these variables (Table 4). The multiple regression model that accounted for the greatest amount of variation indicated that metabolized energy (ME, in kJ) was inversely correlated with temperature, and directly correlated with both weight and weight change as follows:

$$ME = 51.8 + 1.7 \text{ weight (g)} + 14.6 \text{ weight change (g)} - 0.8 \text{ temperature (°C)} - 7.9 \text{ food}$$

where food is treated as a classification variable; oil-supplemented mash = 1, soy-supplemented mash = 2, unsupplemented mash = 3 ($R^2 = 0.56$). Least squares means (estimates of sample means corrected for effects of covariants) ±1 SE indicate that the House Finch metabolizes significantly

TABLE 4
ANALYSIS OF COVARIANCE OF METABOLIZED ENERGY OF HOUSE FINCHES

Source	df	Sum of squares	*F*
Model	12	1677.4	22.9**
Error	106	647.5	
Total	118	2324.9	
Weight	1	26.3	4.0**
Temperature	6	690.4	18.8**
Weight change	1	99.1	16.2**
Food type	2	283.9	23.2**
Sex	1	12.3	2.0
Photoperiod	1	0.003	0.01

** $P < 0.01$.

more energy per day from the oil-supplemented diet (65.7 ± 1.7 kJ) than from soy-supplemented (48.5 ± 1.3 kJ) or unsupplemented diets (47.3 ± 0.8 kJ; see Table 3). Analysis of residuals indicated that there was no further source of temperature-related variation not accounted for, and that the data are linear with respect to temperature. House Sparrows likewise metabolized more of the oil-supplemented mash than the other foods (Table 5).

Arcsine transformations of efficiency ratios were computed and tested using analysis of covariance. As before, the three food types, sex, and photoperiod were treated as covariants. Differences in efficiency due to sex, photoperiod, and weight change were not significant (Table 6), and these data were pooled. Reanalysis using food as a class, and temperature and weight as covariants indicated that energetic efficiency was, by far, most influenced by food type, then by temperature, and lastly by weight, as judged by the portions of the total sums of squares attributable to each of these variables. The "best" multiple regression model ($R^2 = 0.50$) shows energetic efficiency to be inversely correlated with weight and positively correlated with temperature as follows:

$$\text{TEFF} = 1.27 - 0.01 \text{ weight (g)} + 0.003 \text{ temperature (°C)} - 0.08 \text{ food}$$

where TEFF is arcsine-transformed efficiency, and food is treated as a classification variable as above.

Least squares means indicated that the birds used the oil-supplemented mash most efficiently, unsupplemented mash second, and soy-supplemented mash least efficiently. A large amount of variation in energetic efficiency remains unaccounted for by the "best" regression model. How-

TABLE 5

METABOLIZED ENERGY AND EFFICIENCY OF USE OF HOUSE SPARROWS AS MEASURED IN THIS STUDY AND AS PREDICTED FROM EQUATIONS IN BLEM (1973, 1976A)

Temperature (°C)	N	Metabolized energy (kJ)[a]		Efficiency (%)[a]	
		This study	Predicted	This study	Predicted
		Mash			
7	5	96.2 ± 4.0	98.7	72.4 ± 5.4	76.2
14	5	72.4 ± 4.1	86.2	71.5 ± 4.2	75.1
		Soy-supplemented mash			
7	4	94.1 ± 6.2	96.7	64.5 ± 1.9	66.1
14	4	85.8 ± 8.1	90.0	64.0 ± 4.3	64.8
		Oil-supplemented mash			
7	5	146.0 ± 7.3	—	77.9 ± 5.4	83.0
14	6	138.1 ± 9.4	—	79.9 ± 2.8	82.1

[a] Values are means ± 1 SE.

ever, analysis of residuals indicated that there was no further source of temperature-related variation not accounted for, and that the data are linear with respect to temperature.

Energetic efficiencies of House Sparrows were similar to those found by Blem (1976a) using similar diets, and metabolized energies were similar to those found by Kendeigh and Blem (1973) for the winter-adapted House Sparrow (Table 5). Like the finches, the sparrows metabolized by far the larger proportion of calories from the oil-supplemented diet. Also like the finches, calories metabolized from the unsupplemented and soy-supplemented mashes were nearly equal, although the soy-supplemented mash was slightly higher. Although the differences are not statistically significant, House Sparrows seemingly metabolized all three diets at 7 and 14°C more efficiently than the finches.

Food preference.—The percentage of oil-supplemented food chosen at each test temperature was greater than either of the other test foods. Statistical comparisons of preferences are not possible in a conventional fashion; percentages of food selected are interdependent since preference of one food precludes others being selected during individual tests. Even so, the great difference between the amount of oil-supplemented mash and the other types chosen over the series of tests, leads us to seriously question the null hypothesis of no difference in food preference. Oil-supplemented mash constituted 88–92% of the total weight of food eaten, while neither of the other mashes ever amounted to more than 6% of the total.

TABLE 6
ANALYSIS OF COVARIANCE OF EFFICIENCY OF USE OF HOUSE FINCHES[a]

Source	df	Sum of squares	F
Model	12	0.457	17.5**
Error	106	0.220	
Total	118	0.676	
Weight	1	0.015	6.9**
Temperature	6	0.110	8.4**
Weight change	1	0.001	0.5
Food type	2	0.382	87.8**
Sex	1	0.003	1.3
Photoperiod	1	0.002	0.8

** $P < 0.01$.
[a] The ratio, metabolized energy gross energy intake, was transformed by the arcsine procedure (Zar 1974).

In seed preference tests, finches chose sunflower seeds almost exclusively at all temperatures. At 7°C, sunflower seeds comprised 82.4% by weight of the seeds chosen; at 14°C they comprised 99.3%, at 20°C, 100.0%. Millet comprised the remaining percentage of seeds. No milo was eaten at any temperature.

DISCUSSION

Birds invading new areas must make a variety of adjustments to unfamiliar environments. One of the most serious of these is exploitation of new food sources. In much of the United States, and particularly in centers of human population density, the food placed in bird feeders represents a major nutritional resource which may permit the existence of birds not otherwise capable of finding energy sources. We believe the House Finch is such a species.

The House Finch first appeared in Virginia in 1962 and became a breeding species in the Richmond area by 1978 (Blem and Mehner 1981). Today it is a very common permanent resident in urban areas of central Virginia; nearly every city block in Richmond has a male House Finch singing on territory in the spring. We suggest this rapid spread has been aided by artificial food sources provided by humans and perhaps also by the altered microclimate available around human habitations. In the Richmond area, hundreds of House Finches gather at local feeders and are present throughout the winter. A variety of foods may be found in such feeders, but the commonest ingredients are sunflower seeds, white and red millet, and milo. We are aware of little data regarding the food habits of eastern House Finches, but our impression from field studies is that

the species shows a definite preference for artificial food sources (also see Aldrich and Weske 1978). Under natural conditions we have observed House Finches feeding on the seeds of the sweet gum (*Liquidambar styraciflua*) and on unidentified weed seeds, but such observations are not common.

Without artificial food sources we believe that mid-winter survival of House Finches in the newly colonized part of the range would be difficult. Observations by Elliot and Arbib (1953), Katholi (1967), and Aldrich and Weske (1978) support the notion that present eastern House Finch populations generally are sedentary and subject to mid-winter mortality. In Richmond, during two periods of extreme cold in the winter of 1981–82, there were several reports of House Finch mortality at more than one locality, including one observation of 20–30 dead or dying finches at a single location (perhaps 10% of a wintering flock visiting a local feeder; M. O'Bryan, pers. comm.). Additionally we have observed that the number of finches visiting feeders in the Richmond area decreases over winter (unpubl.).

Evaluating the nutritional quality of wild bird food has only recently been attempted and we are aware of only a few studies that provide useful information on nutritional quality of natural foods for small passerines. Willson and Harmeson (1973) suggested that seeds may be selected according to east of handling, but in their study, Cardinals (*Cardinalis cardinalis*) chose foods with higher caloric content at lower ambient temperatures. No correlation was found between energetic efficiency and seed preference. Blem (1976a) found significant relationships between food composition and energetic efficiency in the House Sparrow. Specifically, there is a strong positive correlation between energetic efficiency and fat content of food and a negative correlation between protein content and efficiency. Williams and Hansell (1981) found that Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*) metabolizes dried mealworms more efficiently than chick starter mash. Browning (1981) showed that the Field Sparrow (*Spizella pusilla*) and the Cardinal could choose high quality seeds over those of lesser nutritional quality. However, the seeds they used were very different morphologically, and choices may have been due to differences in the birds' ability to handle the different seeds. Several authors have noted a preference of birds for seeds high in fat (Kear 1962, Conley and Blem 1978).

In the present study it appears that the composition of food affected survival of low ambient temperature. No mortality occurred in birds fed the oil-supplemented diet and the ability of finches to extract energy from this food was greatly enhanced in comparison to soy-supplemented or unsupplemented mash. Inspection of metabolic data further illustrates

this. Simple regression equations were computed for birds being fed each of the three foods. It is obvious that the high protein content of soy-supplemented mash interferes with efficiency of utilization at 7°C and metabolic rates of all finches are elevated at 32–35°C. Eliminating metabolic rates at these temperatures, final equations are:

mash	$M = 54.88 - 0.43\ T;$
soy + mash	$M = 61.43 - 0.78\ T;$
oil + mash	$M = 85.52 - 1.19\ T$

where M = metabolism in $kJ \cdot bird^{-1}day^{-1}$ and T = ambient temperature in °C. There is a visible progression of increasing slopes and intercepts that is directly correlated with fat content of the food, and, to a degree, inversely correlated with protein content. It is obvious that much more energy is metabolized from the oil-supplemented food even though its caloric content is not a great deal higher (Table 1).

Metabolized energy of birds fed soy- and oil-supplemented mashes increased at 32°C over measurements at 26°C. Since this did not occur in birds fed plain mash, we suggest that there may have been greater effects of specific dynamic action associated with the supplemented foods (see Blem 1976a). Metabolized energy of finches fed chick mash was similar in the range 26–35°C. These results suggest the thermal neutral zone commonly found in measurements of the standard metabolism of endotherms, but which is relatively unknown in measurements of metabolized energy (West 1962). Salt (1952) found the thermal neutral zone in California House Finches to be 24–27°C. Perhaps increased levels of metabolized energy at temperatures above 30°C reflect heat stress, especially in those birds being fed high protein food with its associated specific dynamic action.

Our data indicate that metabolized energy and efficiency of utilization of House Finches are both significant functions of food composition. Significantly, food type has a prominant effect on body weight of House Finches even when the effects of temperature, sex, and photoperiod are accounted for (Table 2). Metabolized energy and efficiency of utilization were highest on the oil-supplemented diet, presumably because of the ease of assimilation and relatively great efficiency of lipid metabolism in birds (see Blem 1976b). It appears likely that natural selection favors increased handling abilities for those seeds whose availabilities and compositions promote survival and we believe that this is true in the case of the eastern House Finch. Aldrich (1982) has shown that the eastern race of the House Finch has a larger average bill size than the parental stock. It is logical that those individuals best able to handle sunflower seeds, a

large food particle relative to other foods available to the House Finch, would be those birds with larger bills (see Willson 1971).

Our evidence for the relationship between food preference, cold tolerance, and bill size in House Finches is, of course, not direct. We have shown: (1) food composition is extremely important in the efficiency with which House Finches extract energy from food; (2) foods high in lipid are more efficiently used; (3) cold tolerance is enhanced by foods high in lipid; (4) eastern House Finches prefer foods high in lipid, including sunflower seeds; and (5) survival of extreme cold weather in mid-winter is a particular problem of recently established eastern House Finch populations. Dawson et al. (1983) also indicate that eastern House Finch populations are in the midst of evolution of increased cold tolerance. We have not shown a correlation between bill size and efficiency of handling sunflower seeds, although it has been suggested many times that bill size and size of food items are correlated (see Willson 1971).

SUMMARY

The eastern race of the House Finch (*Carpodacus mexicanus*) tolerates low winter temperatures very poorly. Laboratory tests indicate that their metabolism and cold tolerance is, at least partially, a function of food composition. In the laboratory, oil-supplemented chick mash was preferred over soy-supplemented or unsupplemented mash and was more efficiently metabolized. House Finches select sunflower seeds over millet and milo and this preference may be related to the distinctly higher fat content of the former. Evolution of larger bill size in the eastern race of the House Finch may be due to preference for sunflower seeds at bird feeders in winter, increased cold tolerance as a result of this choice, and the increased range of permanent residency of this species.

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BANDING RETURNS, ARRIVAL TIMES, AND SITE FIDELITY IN THE SAVANNAH SPARROW

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The breeding biology of the Savannah Sparrow (*Passerculus sandwichensis*) has been studied from numerous angles (Dixon 1972, 1978; Stobo and McLaren 1975; Welsh 1975; Weatherhead 1979a, b; Weatherhead and Robertson 1980; Bédard and Meunier 1983). Little attention has been devoted, however, to the temporal pattern of arrival on the breeding grounds, the attachment to specific breeding sites, or the effects of age upon these aspects of reproduction. Patterns such as these have a direct bearing on site and mate selection, processes which are central to current theories of avian mating systems (see Oring 1982 for a recent review). The aim of this study is to summarize and interpret our observations on the biology of the Savannah Sparrow in the context of social organization.

STUDY AREA AND METHODS

The study was conducted from 1976 – 1981 in the Isle Verte National Wildlife Area, 225 km NE of Québec City, Québec, Canada. The 20-ha rectangular study area (10 ha in 1976) consisted of a *Spartina* salt marsh and abandoned field ecotone marked with wooden stakes at 30-m intervals. The two long sides of the rectangle were bound by habitats inhospitable to sparrows (flooded marsh and a highway bordering built-up areas). The study area was used by about 55 breeding pairs and a variable number of bachelor males every year. All males were mist-netted within a few days of arrival, often having been lured to the net by a recording of Savannah Sparrow songs. Over half of the females were also captured, most while incubating or feeding young. The birds were individually marked with colored plastic leg-bands, sexed by the presence or absence of a cloacal protuberance, and weighed. Measurements of wing-length (flattened) were also obtained in 1978 and 1980. Between 1976 and 1980, 281 nestlings were banded at 6 days of age with distinctive "wide-striped" color bands, but none were ever resighted on the study area.

Observations were not equally intensive in all years of the study. Arrival dates were thoroughly monitored in 1978, 1980, and 1981 only. Site fidelity data and banding returns for both sexes, however, are available for all years of the study. Every year, a 100-m-wide band outside each end of the study grid was surveyed occasionally to check for the possible presence of individuals banded within our study area.

The entire grid was visited daily from mid-April (18 May in 1979) until early August (late June in 1979 and late May in 1981). The locations of all activities performed by males (singing, agonistic encounters, foraging, movements, etc.) were recorded on a map of the area (1 cm = 5 m), while the activity patterns of females were mapped in a less detailed fashion. This mapping enabled us to delineate an "activity space" for each individual, the center of which was subjectively determined after excluding the outermost 5% of observation points. Site fidelity of males was determined by comparing the center of the activity space during territory establishment (1–15 May) in one year with that used at the same stage in the following year. Fidelity was measured in terms of the distance (m) between two such

TABLE 1

RETURN RATES OF ADULT MALE AND FEMALE SAVANNAH SPARROWS KNOWN TO BE AT LEAST 1 YEAR OLD WHEN BANDED DURING THIS STUDY

	No. banded		No. returning 1–4 years after banding							
			1		2		3		4	
Year banded	M[a]	F[a]	M	F	M	F	M	F	M	F
1976	24	11	11	5	9	1	4	1	1	0
1977	59	33	19	10	9	2	6	0	1	0
1978	61	34	21	13	14	7	6	3	—	—
1979	25	22	9	5	4	2	—	—	—	—
1980	53	22	26	5	—	—	—	—	—	—
Total	222	122	86	38	36	12	16	4	2	0
% returning			38.7	31.2	21.6	12.0	11.4	5.1	2.5	0

[a] M = males; F = females.

points from successive years for a given individual. For females, nest location (and exceptionally, the center of the activity space) was used to assess site fidelity between successive years. Statistical procedures followed Siegel (1956), and Sokal and Rohlf (1981).

RESULTS

Banding returns.—Of 344 breeding adults banded during the study, 167 returned for at least one (and a maximum of four) additional breeding season(s). The slight tendency for males to return at a higher rate than females the year following banding (Table 1) was not statistically significant, whether using a conventional frequency analysis ($\chi^2 = 1.65$, df = 1, $P = 0.20$, all years combined) or a multivariate log-linear model (Bishop et al. 1975). In the latter analysis, we found no interaction between year, sex, and status (returns at least 1 year or does not return) ($\chi^2 = 4.9$, df = 4, $P = 0.30$).

Since observations were not conducted after 1981, only the cohorts banded in 1976 and 1977 can be used to obtain a complete estimate of adult mortality. Assuming that all this cohort had disappeared by 1982, the weighted annual mortality rates (Farner 1955) are 0.55 and 0.69 for 1976 and 1977, respectively. Therefore, in any given year, first-year birds made up the highest proportion of the breeding population. No bird banded either as a nestling or as an adult was ever observed settling in the 100-m band at either end of the study area.

Arrival dates.—The first male Savannah Sparrows arrived between 19 and 24 April. In 1978, the arrival period was protracted, with an average of 4.4 new males appearing in the study grid each day from 23 April until

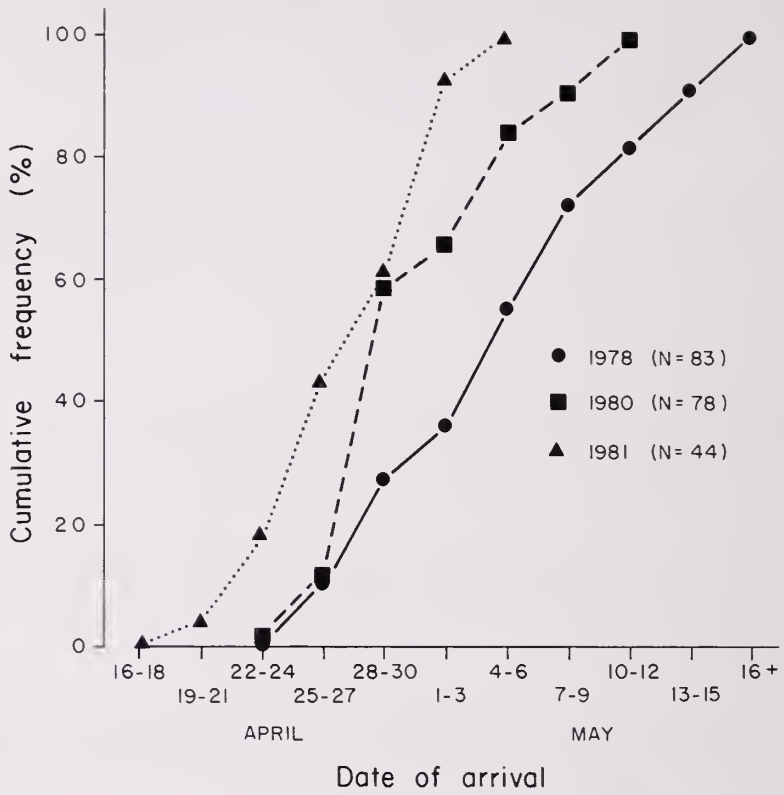

FIG. 1. Cumulative number of male Savannah Sparrows arriving at Isle Verte from mid-April–mid-May for 3 years in which the study area was surveyed daily during the settlement phase.

16 May. By then, all males had established a territory (Fig. 1). The 1980 season showed a different temporal pattern of male arrival: a sudden wave of 27 individuals arrived 29 April, accounting for 35% of all the territorial males that year. In 1981, the daily flow of incoming males was steadier than in 1980, except for a wave of 13 birds that appeared on 1 May. The population build-up of males in 1981 spanned 16 days, as opposed to 19 days in 1980 and 24 days in 1978. The Kolmogorov-Smirnov two-sample test (Siegel 1956) was used to examine differences in the distributions of arrival dates. The pattern of arrival was significantly more protracted in 1978 than in 1980 ($D = 0.313$, $N = 83,78$, $P < 0.001$) and more spread out in 1980 than in 1981 ($D = 0.329$, $N = 78,44$, $P < 0.01$).

The arrival dates of females were difficult to record as they were se-

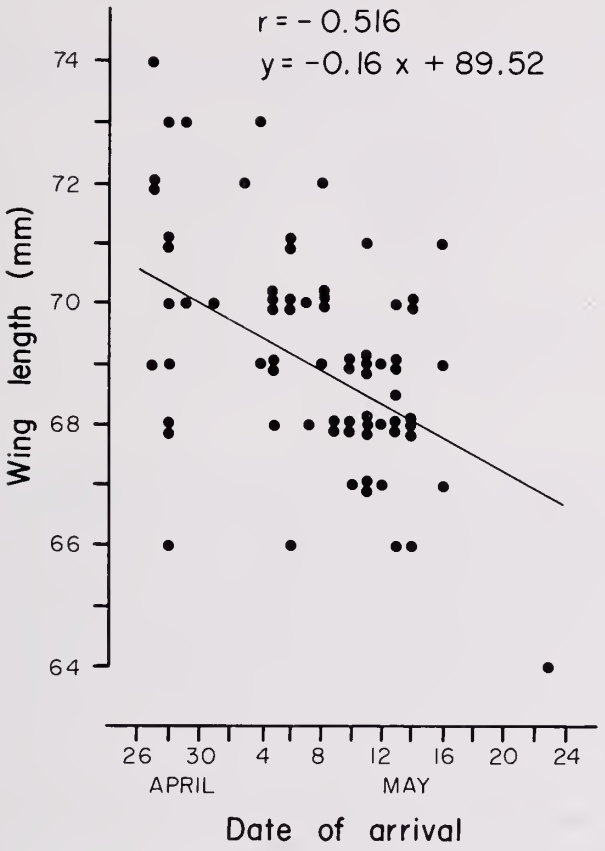

FIG. 2. Wing-length in relation to date of arrival for male Savannah Sparrows at Isle Verte during 1978 (includes 66 first-year males and 12 previously-banded older males).

cretive and frequently escaped notice. Females were first seen 18, 12, and 20 days after the first males in 1978, 1980, and 1981, respectively.

To establish whether wing-length increases with age, we examined a sample of 15 males that had been recaptured over a period of 1–3 years. Twelve individuals were re-measured the year after banding and three others were re-measured 2 years after banding. Wing-length increased significantly between captures by an average of 1.7 mm ($t = 3.9$, N = 15, $P < 0.0025$, one-tailed t-test for paired comparisons, Sokal and Rohlf 1981).

This indicator of age was thereby used in testing the effect of age on

TABLE 2
AVERAGE WING LENGTH (MM) OF UNBANDED MALES AND OF RETURNING BIRDS FOR 1978 AND 1980

Year	Previously-banded returning males $\bar{x} \pm SE$	Unbanded males $\bar{x} \pm SE$	Student's t (one-tailed)
1978	70.8 ± 0.5 (N = 12)	68.9 ± 0.2 (N = 62)	2.85[a]
1980	71.4 ± 0.8 (N = 7)	69.5 ± 0.2 (N = 51)	3.46[b]

[a] $P < 0.005$.
[b] $P < 0.0005$.

male arrival dates. In 1978, earlier-arriving males had longer wings ($r = -0.516$, N = 72, $P < 0.01$, Fig. 2), i.e., older males arrived earlier that year. The significance of this correlation remained unaffected following removal of the particularly short-winged individual from the analysis (without outlier, $r = -0.456$, N = 71, $P < 0.01$). In 1980, we obtained accurate arrival dates for 78 males (unbanded and returning), but only seven of the 34 older banded males were recaptured for wing measurement. Therefore, we could not expect to detect a significant correlation between wing-length and arrival date for that year ($r = -0.095$, N = 58, $P > 0.05$).

The wing-length data also suggested that unbanded newcomers were, on the average, smaller (thereby younger, see above) birds and thus probably first-year males. In both 1978 and 1980, these birds had a significantly shorter average wing-length than the previously-banded returning males (Table 2). Therefore, we grouped arrival dates according to these two size/age categories (unbanded vs banded) and calculated two frequency distributions as in Fig. 1. The span of arrivals of the unbanded first-year males was significantly longer than that of older returning birds in 1978 (Kolmogorov-Smirnov test, D = 0.3, N = 55,28, $P < 0.05$). Again, no significant difference emerged in 1980 (D = 0.12, N = 5,28, $P > 0.05$) or in 1981 (D = 0.20, N = 12,33, $P > 0.05$). The average arrival date was significantly earlier for banded males in 1978 (3 May vs 7 May, $t = 2.82$, df = 81, $P < 0.01$), but not in 1980 ($t = 1.60$, df = 76, $P > 0.05$), nor in 1981 ($t = 0.36$, df = 47, $P > 0.05$).

Site fidelity.—Of 344 banded sparrows, 167 settled in the study area for two or more successive breeding seasons. The distance moved by these individuals between successive seasons was small; 80% of all the moves were less than 60 m, which represents the average diameter of territories

TABLE 3

THE NUMBER OF BANDED SAVANNAH SPARROWS MOVING DIFFERENT DISTANCE CATEGORIES BETWEEN SUCCESSIVE BREEDING SEASONS[a]

	Distance (m)																Total	
	0–20		21–40		41–60		61–80		81–100		101–120		121–140		141+			
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
First move after banding	24	5	29	13	10	9	3	2	4	1	2	1	2	0	11	1	85	32
All subsequent moves	12	2	18	1	5	3	2	0	3	1	0	1	0	0	1	1	41	9
Total	36	7	27	14	15	12	5	2	7	2	2	2	2	0	12	2	126	41

[a] Data are combined for all years of the study (1976–1981).

in our study area (Bédard and LaPointe, unpubl.). No difference was found between the sexes (Kolmogorov-Smirnov two-sample test; $D = 0.20$, $N = 126$ males, 41 females, $P > 0.05$, Table 3). There was no significant difference between first moves after banding and all moves in subsequent years for either males or females (Table 3, males: $D = 0.15$, $N = 85,41$, $P > 0.05$; females: $D = 0.24$, $N = 32,9$, $P > 0.05$).

Social context and breeding success may also influence site fidelity. However, the presence or absence of a nesting attempt in a given year did not influence the distance moved in the following season by males or females (Kolmogorov-Smirnov test; males: $D = 0.16$, $N = 74,52$, $P > 0.05$; females: $D = 0.09$, $N = 32,9$, $P > 0.05$). Likewise, males or females with breeding failures did not move farther the next year than those who succeeded in fledging young (males: $D = 0.15$, $N = 18,52$, $P > 0.05$; females: $D = 0.05$, $N = 10,20$, $P > 0.05$). Finally, both males and females remained just as attached to their site following a change of mate than if they had remained with the same partner in the succeeding year (males: $D = 0.26$, $N = 17,12$, $P > 0.05$; females: $D = 0.33$, $N = 9,15$, $P > 0.05$). In contrast, moves that took place between two successive nesting attempts within the same breeding season were always shorter than moves between seasons (males: $D = 0.22$, $N = 48,126$, $P < 0.05$; females: $D = 0.40$, $N = 35,41$, $P < 0.01$).

DISCUSSION

The lack of differential return rates between male and female Savannah Sparrows in this population agrees with Dixon's (1972) observations on Kent Island for the same species. This contrasts with the significantly lower female return rate in a number of monogamous passerines that nest

in open-ground habitats, such as the Clay-colored Sparrow (*Spizella pallida*) (Walkinshaw 1968, Knapton 1979), the Field Sparrow (*S. pusilla*) (Best 1977), the Seaside Sparrow (*Ammospiza maritima*) (Post 1974), and the Song Sparrow (*Melospiza melodia*) (Nice 1937).

More perplexing than differences in average arrival date for the population as a whole are differences in the temporal pattern of arrivals among years. In boreal latitudes, there should exist a premium on early spring arrival. This does in fact seem to be a fairly universal trait in passerines (Nice 1937, Walkinshaw 1968, Best 1977), generally seen as a result of intrasexual selection. Therefore, one would have predicted that the delayed arrivals in the late 1978 season would have been accompanied by influxes of males compensating for the delay in the migration. To the contrary, this pattern of arrival was exhibited in the 2 early years.

The significant correlation between wing-length and arrival date was based only on the 1978 data, when a high proportion of older males were recaptured and when arrivals were spread out. In 1980 and 1981, there was less effort to recapture returning males; this and the short time-span of male arrivals prevented us from detecting any such trend.

The effect of age on arrival date has been examined in other passerines. Walkinshaw (1968) concluded that "older" male Field Sparrows returned earlier in the spring, but Best (1977) was unable to substantiate this finding in the same species. Catchpole (1972) also found that older male *Acrocephalus* warblers were always the first to settle back on their territories in the spring, although they were not necessarily the first to attract a mate (Catchpole 1980).

Males arriving earlier might increase their chances of obtaining a better territory. Since returning Savannah Sparrows are remarkably site faithful (see also Dixon 1972, Stobo and McLaren 1975), this can obviously not work. The premium on early spring arrival, if it exists at all at Isle Verte, must therefore serve an alternative purpose, such as to extend the breeding season. This would be advantageous in an area where half of the first nesting attempts end in failure (during the years 1977, 1978, and 1980, 66 of 133 [49.4%] first attempts failed [Bédard and LaPointe, unpubl.]).

The existence of site fidelity raises the question of whether the birds are optimizing their choice of breeding location. If such optimization were occurring, then we should witness individual movements towards new sites in successive years, at least by birds that were forced to occupy "poor" locations during a given season (where nesting attempts failed). For instance, late-arriving first-year males are known to squeeze between already established birds (Bédard and LaPointe, unpubl.). In the following year, they should try to improve their situation by choosing a more favorable location, perhaps following an earlier arrival. The results shown

here indicate that this does not occur and Oring (1982) offers an explanation for this phenomenon. Under conditions of low environmental stability, lack of ability to assess habitat quality, or short life expectancy, "the advantages of site fidelity may more than compensate for possible advantages of moving to territories of apparently higher quality," (Oring 1982:35). The Savannah Sparrows we studied appear to adopt this alternative strategy. As an example, the late-arriving (20 May 1977) male 065 returned to the same site for 5 years in a row, despite the fact that he never even managed to attract a female. Several males also remained faithful to the same location despite a string of successive breeding failures within and between seasons. Both Searcy (1979) and Best (1977) have noted instances of passerine males similarly passing up opportunities of moving to "better" territories.

Therefore, site selection by male Savannah Sparrows after their arrival on the breeding grounds at Isle Verte appears to be influenced primarily by previous occupancy. The same seems to apply to females, although our sample sizes are smaller. Female site fidelity is further supported by the fact that female return rates equal those of males. This site fidelity feature is, of course, not a new finding (e.g., Darley et al. 1977, Freer 1979, Harvey et al. 1979, and others); in the Field Sparrow, Walkinshaw (1968) and Best (1977) found likewise. Even in polygynous Red-winged Blackbird (*Agelaius phoeniceus*), Nero (1956) made a strong case for site fidelity, but, except for Searcy (1979), few others have associated this characteristic with Red-winged Blackbirds.

SUMMARY

The Savannah Sparrow (*Passerculus sandwichensis*) was studied at Isle Verte, Québec, during the breeding season from 1976–1981. The temporal arrival pattern of males varied markedly between the 3 years of the study for which we had complete data: the time-span of arrivals diminished from 24–19–16 days for 1978, 1980, and 1981, respectively. Wing-length was found to be an indicator of age. During the only year with complete data we found that older (longer-winged) males arrived earlier. Birds banded as nestlings (N = 281) never returned to the study area to settle as breeders. Birds having bred once in the study area were never found to settle elsewhere (i.e., in a 100-m belt adjacent to the area). Site fidelity was evaluated by comparing the position of the activity spaces occupied by known individuals at equivalent periods of successive seasons; 80% of all moves were less than the average diameter of a territory at Isle Verte (60 m). The distance moved did not vary between sexes, nor did it differ when nesting was not attempted, when nesting failed, or, when change of mate occurred. Strong site fidelity in this population of Savannah Sparrows is viewed as an alternative strategy to habitat quality re-assessment upon spring arrival.

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STRUCTURE AND DYNAMICS OF COMMUNAL GROUPS IN THE BEECHEY JAY

Ralph J. Raitt, Scott R. Winterstein, and John William Hardy

Studies of avian cooperative breeding now have progressed to the stage at which attempts have been made to formulate generalizations concerning its adaptive significance and mode of evolution (Brown 1969, 1974, 1978, 1980, 1982, 1983, in press; Ricklefs 1975; Fry 1977; Emlen 1978, 1982a, b; Gaston 1978; Koenig and Pitelka 1981; Ligon 1983). Prominent among the studies contributing to the success of those who attempt generalization are several on New World jays, including especially those of Brown (1963, 1970, 1972; Brown and Brown 1980, 1981a) on the Mexican or Gray-breasted Jay (*Aphelocoma ultramarina*) and of Woolfenden (1973, 1975, 1978, 1981; Woolfenden and Fitzpatrick 1977, 1978; Stallcup and Woolfenden 1978) on the Florida Scrub Jay (*A. c. coerulescens*).

The black-and-blue jays of the subgenus *Cissilopha*, genus *Cyanocorax*, are a group of several allopatric forms of Mexico and Central America, all of which breed cooperatively (Hardy 1976; Raitt and Hardy 1976, 1979; Hardy et al. 1981). In a comparative study of the behavior and ecology of this group we gave particular attention to the relationships of population structure and dynamics to cooperative breeding in the Beechey Jay (*Cyanocorax beecheii*), the northernmost of the forms and apparently the only one in which some breeding pairs regularly have helpers and others do not.

We studied a population of *C. beecheii* from 1974–1978 near Mazatlan, Sinaloa, Mexico. As described in an earlier paper (Raitt and Hardy 1979) and confirmed by the findings of an additional two years of study (1977–1978), these jays occupy dense, lowland deciduous forest, in a highly seasonal climate with a continuous very dry period that lasts about 6 months. They live throughout the year in groups of 2–6 fully grown birds (yearlings or older), on large territories (25–43 ha) that they defend against members of other groups. Parenthood within a group is confined to a single adult ($\geq$3 years old) member of each sex. No more than one successful nesting attempt is made by a breeding pair each year; renesting was observed only after failure of a first attempt. All members of a group help to defend the nest and to feed nestlings and probably all participate to some degree in nest construction and care of fledglings. We ascribe the relatively large body size, large territory, and relatively low reproductive output in this species to relatively low productivity of food in a seasonally severe and generally dry climate (Raitt and Hardy 1979).

We examined various hypotheses that form the core of developing theory concerning the evolution and adaptive significance of cooperative breeding in birds. These include advantages and disadvantages of helping to both helpers and breeders, genetic relatedness within breeding groups, age of helpers and breeders, the mode by which helpers attain breeding status, and other aspects of cooperative breeding.

METHODS

We captured and marked jays with distinctive combinations of colored leg bands and plastic flags (see Raitt and Hardy 1976). Ninety-six birds were marked, the majority (N = 63) as nestlings. It was difficult to capture fully grown birds and a few remained unmarked. The stability of group composition, obvious morphological age variation, and the small number of unmarked individuals per group (usually no more than one) permitted most of the latter to be individually identifiable.

We observed the jays' activities, including movements; located as many nests as possible; followed progress of nests; and observed activity at and around them. In conducting timed observations of activity at nests, we sampled opportunistically, but at all nests we made as many observations as possible at different times of day in each stage of the nest cycle. Nests of nearly all known groups in each year were found and fates of nesting efforts determined; a small number of late, second attempts were still in progress on termination of our field work for the respective summers.

RESULTS

Group composition and stability.—As indicated in the earlier paper, each breeding-season group included at least one adult member of each sex; some consisted only of such a pair but most also included helpers (Fig. 1, Appendix). Helpers included individuals of all three major age classes of fully grown birds: yearlings, 2-year-olds, and adults. An apparent year-to-year trend of increasing size of groups is not statistically demonstrable by Chi-square test ($\chi^2 = 12.24$, df = 16, $P > 0.5$).

Several of the groups, most of which had a considerable degree of continuity of individual membership, occupied the same territory year after year (e.g., groups A, B, E, Fig. 1). Some groups, however, dissolved. Destruction of habitat was implicated in the dissolution of groups A and F; D and G disintegrated and H and I simply disappeared, all without severe habitat disturbance. In D and G one member of the previous year's breeding pair disappeared, and presumably died, and the surviving members joined other groups, as breeders. It is likely that the proximate cause of the breakup of groups D and G was the death of a breeder, who could not be replaced by an adult from within the group.

Most of the changes in group membership were caused by recruitment of young by reproduction and death of group members rather than by intergroup movement. Of the 46 fully grown birds known to have been added to groups, 35 were offspring of the respective breeding pairs, and

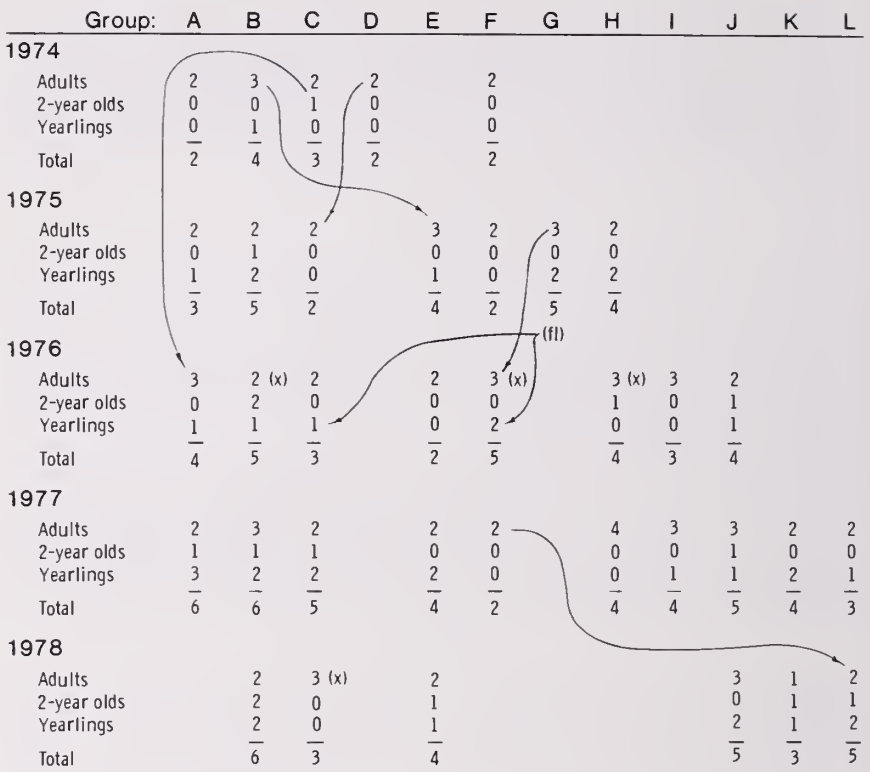

FIG. 1. Composition of Beechey Jay breeding-season groups, 1974–1978. Each arrow indicates change in group membership of an individual bird; (x) indicates the immigration of a bird from an unknown source. Two fledglings (fl) from group G in 1975 emigrated to groups C and F, respectively.

only 11 immigrated. Of 84 birds that disappeared from their groups, 75 disappeared permanently from the study and only seven joined other known groups (see Fig 1, Appendix). The remaining two were observed subsequently on the study area but their group affiliation remained uncertain.

Three of the seven switches between known groups were by adult males, one of which (OO) switched once (group D to group C, 1974–1975), the other of which (OB) switched twice (group G to group F, 1975–1976, then to group L in 1978). One was by an adult female, AA, (B–E, 1974–1975); one by a 2-year-old (OA), sex unknown (C, 1974–A, 1976); and two by fledglings, one a male, RV, (G–C), the other of unknown sex, VG, (G–F).

All four of the birds that immigrated from unknown sources (indicated

TABLE 1
RELATIONSHIP BETWEEN HELPERS AND MEMBERS OF BREEDING PAIRS

Year	Total helpers	No. birds helping breeding pairs				
		Both parents	One parent	Probable parents[a]	Only non-parents	Birds of unknown relation
1976	14	2	5	3	2	2
1977	23	12	2	6	1	2
1978	14	4	6	2	0	2
Total	51	18	13	11	3	6

[a] Includes only birds banded as yearlings in groups with no known past history; birds banded as 2-year-olds or as adults in groups with no known past history were placed in the unknown relation category.

by (x) in Fig. 1) were adults, two females and two of unknown sex. One of the females (O/Wr) was a breeder in her first year after immigration; the other (RG) became a breeder after helping for 1 year. The other two (XX group C and P/B) were helpers for 1 and 2 years, respectively. In summary, adults of both sexes predominated among individuals known to have moved to different groups (8 of 11). Five of such adults were breeders in their first appearance in the new group but three were helpers.

Of eight instances in which one of the breeders disappeared and was replaced, the replacements were immigrants in four (O/Wr, OO, and OB twice). In two cases, the replacement was a bird that had immigrated previously: RG as an adult the year before and RV as a bird-of-the-year 2 years before. In the seventh instance, replacement was by a group member (see account of history of PV below). In the final case, replacement was by an adult (XX group E) that served as an adult helper in the previous year, but for whom we have no juvenile history.

Although parent-helper kinship was uncertain or altogether unknown in a number of instances, most helpers definitely were associated with at least one parent when protecting and feeding younger siblings or half-siblings (Table 1). But three definitely contributed to the rearing of less closely related individuals.

We found only one case of mating of close relatives; in 1978 PV mated with her presumed father, WV. PV was banded as a yearling in 1975 when she was a member of group B in which WV was the male breeder (Appendix). She was presumably one of the surviving members of a group of nestlings from a nesting attempt still in progress at the conclusion of our field work in 1974; WV was the male parent in that attempt.

Attentiveness.—On the average, some jay visited the nest to feed the nestlings once every 18 min (1374 visits in 405 h of observation). Breeding

TABLE 2
FEEDING VISITS BY AGE CLASS, SEX, AND ROLE

Age class	Sex	Role	x̄ % of visits	x̄ visits/h
Adult	female	breeder	24	0.84
Adult	male	breeder	35	1.24
Adult	female	helper	4	0.58
Adult	male	helper	1	0.50
2-year-old	?	helper	8	0.52
Yearling	?	helper	28	0.84

males accounted for the majority of the feeding visits, followed by breeding females and yearling helpers, and then by other classes (Table 2). The percentage of the feeding visits made by the breeders decreased as the number of helpers increased (Fig. 2; Fig. 3, groups B and E). Proportional contributions of breeding males varied more, both among years and among groups, than did those of breeding females. Although in groups consisting of only two or three, breeding males accounted for the majority of the feeding visits (Fig. 3, groups E, D, C, A), such males appeared to benefit most by the presence of yearling helpers (Fig. 3, groups B and E).

Individual birds did not account for an increased percentage of the feedings as they matured. Individuals made fewer feeding visits as 2-year-olds than they did as yearlings; birds helping as adults made no more visits than they had as 2-year-olds.

A multiple regression analysis, using dummy variables and the improvement concept (Draper and Smith 1966), was used to test for relation between variation in number of feeding visits per hour and (1) age of nestlings, (2) number of nestlings, and (3) number of feeders. Whereas both age and number of nestlings showed little relationship with feeding rate, the regression coefficient associated with number of feeders was significant at the 0.03 level ($F = 4.92$, $df = 1, 37$). A similar, but more extensive, regression analysis by Brown et al. (1978) on Grey-crowned Babblers (*Pomatostomus temporalis*) showed that metabolic demands of the nestlings and environmental factors had a greater effect on feeding rates than did the number of helpers. The same could be true for Beechey Jays.

All members of each group also assisted in defending nestlings and fledglings and defending the territory from other groups. The manner in which the vicinity of the nest (within about 10–15 m) was patrolled apparently depended upon group size. The five birds of one group were

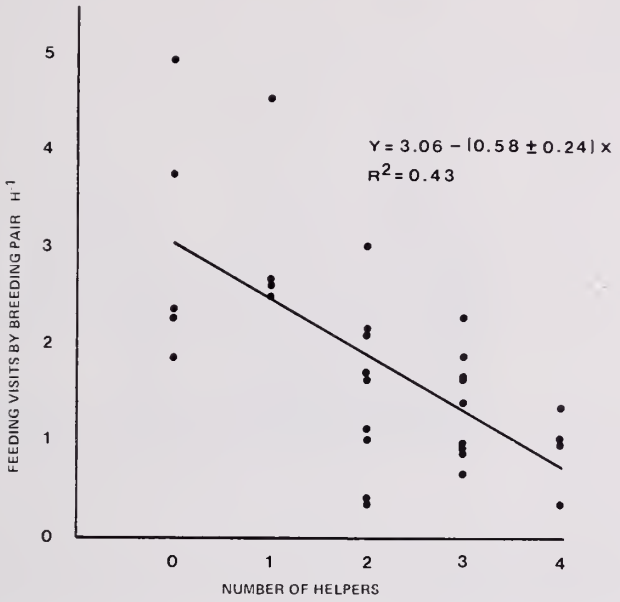

FIG. 2. Relationship between feeding rates by members of breeding pairs of Beechey Jays and the numbers of helpers. The value 0.24 is the 95% confidence interval for the estimate of the slope (−0.58).

observed on various occasions to station themselves as follows: one bird was at each of the corners of a square centered on the nest, while the breeding female was on the nest. In a group made up of only a breeding pair, defense was different. When both birds were present, one positioned itself near the nest while the other moved about the vicinity, stopping at various points. If only one bird was present, it moved about, stopping briefly at numerous points. Regardless of group size or the manner by which they patrolled, at least one bird was almost always present near the nest.

Based on actual observations of predation and on strong circumstantial evidence, the most important nest predators were Mexican beaded lizards (*Heloderma horridum*), a variety of snakes, and Magpie-jays (*Calocitta colliei*). Predators of lesser importance included squirrels, hawks, owls, crows, and possibly jaguarundi cats (*Felis yagouaroundi*). Most predators were driven off by the cooperative mobbing efforts of all group members. Actual physical encounters were rare because most predators retreated from the mobbing birds. However, on at least two occasions jays dived

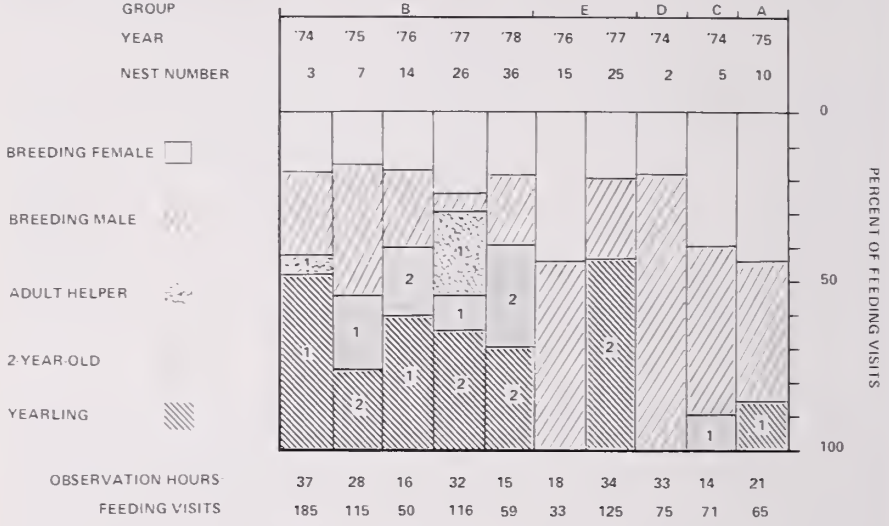

FIG. 3. Changes in percentage of feeding visits by age-class and role of members of Beechey Jay breeding season groups. Numbers within marked columns represent the number of helpers in that age-class in that year.

at squirrels and knocked them out of the nest tree. Jays also frequently mobbed human observers, mirrors used to observe nest contents, or mist nets when any of these were at or near the nest.

Unlike predators moving along the ground and perched birds of prey, avian predators on the wing were rarely mobbed; they were immediately, silently, and directly attacked and driven away. The extreme quickness with which avian predators could fly to a nest, seize a nestling, and fly off probably accounts for this different manner of attack.

Reproductive success.—Each group attempted only one nest at a time and did not nest again after successful fledging. An unsuccessful first nesting attempt was generally followed by a second attempt; no third attempts were observed. Clutch-size varied from three to five ($\bar{x}$ = 4.2, N = 25) and the number of nestlings from one to five ($\bar{x}$ = 3.2, N = 34). The mean number of fledglings produced per group per year was 2.3 (range: 0–5, N = 22); variation among years was remarkably low, with extremes of 2.0 and 2.5. Using Green's (1977) modification of Mayfield's (1961, 1975) method, we calculated 0.29 as the overall probability that any egg would produce a fledgling.

Of 99 eggs, 15 were lost prior to the end of incubation, 13 when entire clutches disappeared; two were single losses from different nests. As no egg losses were attributable to either storms or abandonment, all 15 were

TABLE 3
REPRODUCTIVE SUCCESS AS RELATED TO THE PRESENCE OF HELPERS

	Groups without helpers (N[a])	Groups with helpers (N)	P[b] t-test	P[c] Fisher's
$\bar{x}$ fledglings produced/nest	1.93 (7)	2.32 (27)	>0.25	=0.41
$\bar{x}$ yearlings produced/nest	0.96 (7)	1.35 (22)	≈0.10	=0.81
$\bar{x}$ fledglings surviving to 1 year of age/nest	1.19 (5)	1.84 (16)	≈0.06	=0.52

[a] Number of nests.
[b] Pooled t-test; $\sqrt{x + \frac{1}{2}}$ transformation was employed (see Sokal and Rohlf 1969, Woolfenden 1975).
[c] Fisher's exact probability test (see Romesburg et al. 1981).

presumably lost to predators. Only 63 of the 84 eggs present at the end of the incubation period actually hatched.

Of 101 nestlings whose fates were known, 40 died and 61 fledged. Of those that died, 25 were lost to predators and 7 died as a result of disease (including parasitism) and/or starvation; the cause of death for the remaining 8 was unknown. Late jay nests (young hatched after the wet season began) lost a significantly greater proportion of nestlings than did early nests (Chi-square = 10.8, df = 1, $P < 0.005$). We have no evidence, for early or late nests, of either nest abandonment or loss of nestlings as a direct result of inclement weather.

Winterstein and Raitt (1983) showed that heavy infestations of parasitic fly larvae could greatly retard nestling growth and development and ultimately be fatal; however, the presence of even large numbers of these subcutaneous parasites did not significantly affect survival to one year of age.

We performed a number of statistical analyses to determine whether reproductive success was related to number of helpers. Spearman rank correlation tests of numbers of helpers versus both numbers of fledglings produced ($r_S = 0.08$, N = 23, $P = 0.72$) and number of young surviving to yearling age ($r_S = 0.27$, N = 14, $P = 0.36$) indicated non-significant relationships. We also compared reproductive output of groups with helpers to that of groups without helpers. As a first step, we employed t-tests on transformed data (Woolfenden 1975); the results (Table 3) indicated a possible significant difference in the number of fledglings surviving to the subsequent breeding season. However, our data (counts having only a narrow range of possible values) are more appropriately examined with a Fisher's exact probability test for $r \times c$ contingency tables (Sokal and Rohlf 1969; Romesburg et al. 1981). (This test, because of the excessive computations required, was not feasible for earlier workers prior to recent development of computer programs.) Results (Table 3) indicate that we

TABLE 4
SURVIVAL RATES FOR DIFFERENT AGE CLASSES OF BEECHEY JAYS

Age at start (years)	No. individuals at risk	No. survivors after 1 year	% survival rate
Fledgling	55	21	38
1	29	14	48
2	10	6	60
3+	73	51	70

have no grounds for rejecting the null hypothesis of no difference in reproductive output between the two sets of groups.

Survival.—We estimated survival rates from the histories of marked birds (Table 4). The apparent trend of increasing survival rate with age was confirmed by Chi-square tests. A survivorship curve based on the rates shown indicated that the expected longevity of a cohort of fledglings of a given breeding season is approximately 10 years. Although data on survival of older age classes are meager, of 11 adults marked in 1974—when they were at least 3 years old—three survived to 1978, when they were no younger than 7 years.

We emphasize that the survival rates of Table 4 are minimum estimates, based on birds known to be alive; other individuals of the various cohorts may have survived after moving out of the study area, although each year we searched unsuccessfully for marked birds in adjacent habitats. A concrete indication that the estimates are low is that they require that each breeding group, on the average, produce approximately six fledglings per year in order to replace the number of adults dying per year. In fact the actual average production of fledglings per group per year was 2.3, little more than one-third of what would be expected. As pointed out above, Fig. 1 indicates a low rate of immigration into the population and thus immigration is unlikely to have accounted for the disparity between measured production and estimated survival.

Not only are the estimates probably lower than the actual survival rates, but the latter might also be atypically low. A substantial proportion of the individuals that disappeared—and were presumed to have died—did so when their groups dissolved after clearing of their habitat. Such dissolution probably resulted in increased rates of mortality and/or emigration.

Stable groups with long known histories probably yield more typical and perhaps more accurate estimates of survival rates. Groups A, B, C,

E, and F were such groups (Fig. 1). From them, over the years of the study, eight adults disappeared, presumed dead, yielding an estimated minimal survival rate of over 79%, as opposed to the estimate of 70% given in Table 4.

DISCUSSION

The principal objective of this study was to answer some fundamental questions concerning the mode of evolution of cooperative breeding in birds. What are the advantages and disadvantages of the helping system to the breeders? To the helpers themselves? Do the interests of parents and helpers coincide? Are they opposed? Are advantages direct? Or are they indirect, involving primarily benefits to kin?

Costs and benefits to breeders.—Positive correlation between presence of helpers and reproductive output is the principal direct benefit to breeding pairs shown in a number of other cooperative species (Florida Scrub Jay, Woolfenden 1975; and others cited in a review by Brown 1978; see also recent experimental evidence of Brown et al. 1982). In the absence of such correlation in this study, we cannot conclude that helpers in Beechey Jays confer an immediate reproductive advantage on the breeding pairs. It is possible, however, that such an advantage could be demonstrated with a larger sample, especially of breeding pairs that had no helpers.

Another potential benefit to the breeding pairs is that, by their efforts at nest building and feeding and protecting young, helpers might have contributed to the survival and thus to the residual reproductive value and lifetime fitness of the breeders. Pertinent to this possibility is the relationship between number of helpers and feeding rate of parents. For each additional helper, the breeders made, on the average, one less visit each 2 hours. Presumably, the lower parental feeding rates result in a substantial saving of time and energy, and lower the risk of predation.

Helpers also participated actively in defense of nests and fledglings against predators, and again it is logical to presume that their assumption of a portion of the risks inherent in such defense reduced risks to members of the breeding pair. Whether these apparent benefits to the breeders did in fact increase their survival and overall reproductive value can only be inferred in the absence of adequate data on survival in relation to number of helpers. It has been shown that Florida Scrub Jay breeders with helpers do indeed survive longer than those without helpers (Stallcup and Woolfenden 1978).

The presence of helpers on the territory has been viewed by others (e.g., Brown 1974; Gaston 1978; Ligon 1981; Emlen 1982a, b) as a form of

extended parental care. As most helpers are offspring of the breeders, benefits derived by the helpers (see below) inevitably provide an additional increment to the fitness of the breeders.

Costs to the Beechey Jay breeders of the helping system appear minimal, in contrast to the situation described by Zahavi (1974) among others. Helpers consistently behaved inconspicuously in the vicinity of the nest—except when mobbing—and were indistinguishable in this behavior from breeders. Had helpers been a serious liability to breeders, we might have expected to see aggression toward them by the breeders (Emlen 1982b), but no such agonism was evident. Any cost to the breeders of the use by helpers of the resources of the territory were at least partially offset by helper participation in territorial defense.

Costs and benefits to helpers.—A full discussion of the costs and benefits to helpers requires a consideration of those entailed first, in remaining on the natal territory and second, in behaving as a helper (Brown 1978, Emlen 1982b). The obvious primary cost of staying and helping is that of foregoing breeding and expending time, energy, and risk of predation to rear young that are usually less closely related to them than their own offspring would be (Brown 1974, Koenig and Pitelka 1981, Emlen 1982a, and many others). Partly offsetting this cost is the substantial probability that the young helper will itself eventually breed. This probability is a consequence of the survival rates and the dynamics of the groups. First, it can be calculated readily from the survival rates of Table 4 that a yearling helper has at least a 29% probability of reaching adulthood (at least three years of age). Once a bird reaches that age the probability that it will breed is high. There is a 30% chance that, in its group in any given year, at least one member of the previous year's breeding pair will have disappeared. Furthermore, the probability that an adult will have an opportunity to breed is increased by the possibility of emigrating to a neighboring group in which such an opening has occurred; as shown, birds move rather freely between groups to fill such openings. The overall probability of an adult having an opportunity to breed is illustrated by the fact that 85% (29 of 34) of all known individual adults were breeders in at least one season. Only one adult was known to have died before having bred; the other four non-breeders were still alive at the end of the study and may eventually have bred. It is also relevant that two known birds bred in a minimum of five consecutive seasons and 11 more bred in at least three seasons. Of the remaining 16 birds, two were known to have bred in only 2 years, the remaining 14 were either breeders when the study started or when it ended and probably bred in more than the one or two seasons we recorded. Clearly, birds that survived to become breeders enjoyed a substantial reproductive value.

A more important factor mitigating the presumed cost of foregoing breeding by the young helper is the low probability that it would be able to breed successfully should it leave its natal territory and attempt to nest elsewhere. The choices faced by such a youthful member of a cooperatively breeding species were discussed first by Selander (1964) and Brown (1969) and recently by Koenig and Pitelka (1981) and Emlen (1982a). Unlike some cooperative breeders, Beechey Jays do not appear to have highly specific habitat requirements and the extent of their habitat, although shrinking (Raitt and Hardy 1979), was not historically highly limited. Nevertheless, observations on our study area and elsewhere within the range of the species indicate that virtually all obviously favorable habitat (see Raitt and Hardy 1979 for habitat description), and some apparently less favorable, is included in permanent territories defended by established breeders, usually with helpers. As pointed out by Selander (1964), Brown (1969), Koenig and Pitelka (1981), Emlen (1982a), and many others, in such a situation a young individual would find it nearly impossible to establish a territory on which to breed. In the case of Beechey Jays, whose habitat in the later half of the nonbreeding season is very dry and low in available food (Raitt and Hardy 1979), it may well be that survival in marginal habitats between breeding seasons is as critical as the problem of finding habitat in which to attempt breeding. Thus the principal benefit to the nonbreeding Beechey Jay of remaining on the territory appears to be that attributed to helpers of other species of birds by Woolfenden (1975, 1981), Woolfenden and Fitzpatrick (1978), Brown (1978), Ligon and Ligon (1978a, b), Ligon (1981) and Emlen (1981) among others; this is that helpers are able to share in the resources of a territory in suitable habitat, defended by a group, until they obtain an opportunity to breed. Supplementary benefits to remaining on the territory are those of membership in a group: cooperation in locating aggregated food sources, warning of and mobbing predators, and defense of the territory (but see Alexander 1974 for discussion of disadvantages of living in a group).

If benefits to the helper of remaining on a territory in which it is not a breeder are relatively clear, benefits obtained by helping behavior (i.e., building the nest, feeding of young, guarding the nest and fledglings, and territorial defense) are less clear. Benefits of helping in two well studied species apparently depend on the manner in which helpers ascend to breeding status. In Florida Scrub Jays nonbreeders may gain their own breeding territory through helping (Woolfenden and Fitzpatrick 1978). Most female helpers that become breeders disperse to other groups to join mature, unmated males. Males on the other hand remain on their natal territories longer than females (and provide more assistance in each season of helping). Most mature male helpers become breeders through obtaining

as their own territory a portion of their natal territory and mating with an immigrating adult female. This "budding" of new territories is made possible by expansion of the original territory as the group increases in size. Thus helpers are envisioned as helping to create their own opportunity to breed by their contribution to the expansion of their natal territory. Although we are hindered in comparing the above system with that in the Beechey Jay by paucity of data on sexual identity, several attributes of the Scrub Jay system are not apparent in that of the Beechey Jay. We did not find a trend of expansion of territories with group size for groups that we knew well. Group A enlarged progressively from 2 to 6 (Fig. 1, Appendix) in a series of years without discernible change in its territory. Group B's territory, with which we were most familiar, underwent some slight changes in size that were not correlated with changes in the size of the group. Concomitantly, we saw no evidence of budding of new territories from old ones.

No instances occurred of a single bird leaving one group to join another single bird of the opposite sex to form a new group. Of helpers that became breeders, female PV remained in her natal group, male RV moved from group G to group C as a yearling and then bred as a 3-year-old, female AA was an adult helper with group B in 1974 and became a breeder in group E in 1975, and female RG immigrated to become an adult helper with group F in 1976 and then a breeder with that group the following year. Thus, two female helpers moved to other groups before breeding, but one male did likewise, and one female remained in her natal group. The sample is small but the behavior of the birds did not conform to the pattern found among Florida Scrub Jays. The histories of two adult male breeders (OO and OB) also failed to conform. The mate of each disappeared (died?) between breeding seasons and each became a breeder in a different group in which the breeding male had disappeared. If the system in Beechey Jays were as in Florida Scrub Jays, these males would have remained on their territories to be mated to dispersing adult female helpers from some other group.

The Green Woodhoopoe (*Phoeniculus purpureus*) also possesses a well-studied, rather elaborate system of dispersal of helpers to become breeders (Ligon and Ligon 1978a, b; Ligon 1981, 1983). Unlike communal jays that have been studied, woodhoopoes apparently suffer high mortality rates and social groups are in a greater state of flux, with new ones being formed rather frequently. Apparently the usual manner of ascendancy of an adult helper to breeding status is for one to disperse along with younger flock mates of the same sex, whom it had helped to rear. "Older helpers clearly gain by helping to produce younger flock mates in that the younger

birds can be 'used' to obtain breeding status for the older (former) helper and . . . care for the older bird's own nestlings." (Ligon 1981:242). The only behavior resembling this that we saw was the dispersal of breeder OB with one of his offspring to group F. No other dispersing Beechey Jay was accompanied by another group member.

In summary, Beechey Jay helpers become breeders either by dispersing to another group or remaining in their natal group but there seems to be no consistent difference between the sexes. The territorial and dispersal behavior of Beechey Jays appears not to be such that helpers increase the probability of becoming breeders by helping to enlarge their territories nor such that they increase the probability that they will have younger sibling helpers to accompany them in dispersal.

Parenthetically, the dispersal pattern seems to contain no particular mechanism that would prevent incest, and indeed the case of PV in group E was an apparent case of a daughter mated to her father. Furthermore, inbreeding may be the explanation of the unusually high proportion (25%) of eggs that failed to hatch in this study (see Koenig 1982).

Helpers may help at the nest in order to gain access to it or to the breeder of the opposite sex for reproductive purposes. Polygamous or promiscuous matings with members of the breeding pair by other group members of one or both sexes have been reported among several cooperatively breeding species, including Acorn Woodpeckers (Stacey 1979, Koenig and Pitelka 1981) and others cited by Emlen (1982b). Among the many studied cooperative jays, such behavior is reported only for the Brown Jay (*Cyanocorax morio*) (Lawton 1979), and Black-throated Magpie-jay (Winterstein, unpubl). We have no evidence of such plural breeding in Beechey Jays. Exceptionally large clutches or ones of heterogeneous appearance were not detected, which would appear to rule out polygyny or female promiscuity. Male helpers could have stolen copulations, but as mentioned previously, we saw no antagonism by breeders toward helpers, which would be expected should such copulations be at all frequent.

Another possibility is that nonbreeders increase their own later effectiveness as parents by helping. Unlike young Brown Jays (Lawton and Guindon 1981) and Florida Scrub Jays (Stallcup and Woolfenden 1978), young Beechey Jays did not increase their feeding rates as they became older, either within their first season as helpers or between that season and later ones. In the closely related southern San Blas Jays (*Cyanocorax s. sanblasiana*), however, in which some individuals less than 3 years old do become breeders, those individuals are less successful than are older breeders (Hardy et al. 1981), perhaps because of less experience as nest attendants. Feeding rate is surely an imperfect measure of potential ef-

fectiveness in breeding; without a better test than our data provide, we cannot draw a firm conclusion as to the possible advantage of experience in helping.

A more likely benefit that the helper gains from helping is that if it becomes a breeder in the same group, it may receive the help of younger birds that it had helped to rear (Brown 1978, Emlen 1982b). In some respects this benefit resembles that described for the Green Woodhoopoe, but it does not involve aid in obtaining breeding status. Four different Beechey Jays became breeders in the same territories in which they had been helpers. One of these (PV) was helped in producing three fledglings in the last year of the study by two yearlings and two 2-year-olds that it had helped to rear (see Appendix, group B). In the other three cases the potential helpers did not survive to the next breeding season to reciprocate when the older helper became a breeder. The fifth known helper that became a breeder did so by changing groups.

Another possible explanation for helping behavior is that it is "payment" (sensu Gaston 1978) for the opportunity to share the resources of the territory and to succeed to breeding status on it (Brown 1969, Koenig and Pitelka 1981). Breeders may not allow nonbreeders to remain on a territory if they do not help. We are compelled to admit that we have no direct evidence for this kind of behavior, but as is usual among cooperative breeders, all nonbreeding Beachey Jays did indeed help and no instance was observed that suggested a breeder's expelling a potential helper. Thus we offer this possibility in large part by default, because we have been forced to reject most other possible benefits of helping.

A final possible benefit of helping to the helper is indirect (sensu Brown 1980), via kin selection. Various students of cooperative breeding in birds have argued either for or against the importance of kin or indirect selection in the evolution of helping (see Brown 1978, 1980, in press; Brown and Brown 1981a, b; Brown et al. 1982; Koenig and Pitelka 1981; Ligon 1981, 1983; Woolfenden 1981), often without convincing tests of their respective hypotheses. While our findings likewise fail to provide such a test, most Beechey Jay helpers did help one or both parents (Table 1). Any resulting gain in the direct fitness of those parents inevitably produced an indirect benefit to the helpers.

CONCLUSIONS

We believe that the Beechey Jay helping system imposes little or no costs to breeders and that they probably gain benefits in increased survival. A larger sample size might also show an increase in annual breeding success. Inclusion of nearly all suitable habitat within territories defended the year around by breeders, usually with helpers, provides the advantage

to young individuals of remaining on their home territory with their parents. This explanation has gained wide acceptance among students of cooperatively breeding birds. Our findings are consistent with three possible explanations for the adaptive advantage to helpers of helping: (1) that they help to rear young that later will become their helpers; (2) that helping is a "payment" to breeders for allowing helpers to remain on the territory; and (3) that the benefits to helpers are indirect. We cannot point to any one of these as more important than the others and believe that all three may be operative. The nature of our conclusions concerning costs/benefits precludes more than passing mention of recent discussions of such characteristics of avian cooperative breeding behavior in relation to general sociobiological theory, which feature conflicting terminology and conclusions (see Brown 1983, in press; Ligon 1983).

Social organization and behavior in Beechey Jays resemble those in Florida Scrub Jays in many respects: some pairs have helpers but some do not; territories are permanent, defended throughout the year; only one pair of adults per territory are breeders in any particular breeding season and a single nesting is the rule, unless the first attempt fails; helpers include all major age classes; and helpers are usually closely related to breeders. On the other hand, two major differences are evident. Unlike Florida Scrub Jays, Beechey Jay helpers do not greatly increase the annual reproductive success of the breeders that they help. And Beechey Jay helpers have a more loosely organized system of dispersal to become breeders, in contrast to the marked differences between sexes and territorial expansion and budding in Florida Scrub Jays. The principal conclusion to be drawn from these contrasts is that a successful system of cooperative breeding in jays need not involve marked increase in breeding success on the part of aided breeders or an elaborate system of eventual dispersal of helpers.

The similarities to Florida Scrub Jays stressed above are in contrast to the marked differences between Beechey Jay ecology and behavior and those of its close relative in the subgenus *Cissilopha*. Variation in the habitat among the forms of *Cissilopha* has been proposed as the explanation for the variation in social behavior (Raitt and Hardy 1979, Hardy et al. 1981). The highly social Southern San Blas Jay occupies habitats that are severely altered by humans and rich in food, whereas the least social Beechey Jay is found in more natural and less productive areas. The other forms of *Cissilopha* are intermediate in both social system and habitat. Variation in habitat also may be related to the differences in dispersal pattern between Beechey Jays and Florida Scrub Jays and Green Woodhoopoes: somewhat elaborate systems of territory budding and group dispersal may require habitat that is more open than that of Beechey Jays.

The dense forest of that habitat may preclude sufficiently close monitoring of adjacent groups.

SUMMARY

Structure and dynamics of breeding groups in the cooperatively breeding Beechey Jay (*Cyanocorax beecheii*) were studied near Mazatlan, Mexico, from 1974–1978. Breeding groups were composed of one breeding adult member of each sex and 0–4 helpers, which varied in age from yearling to adult (3 years or older). Most groups were relatively stable in membership and occupied the same territories throughout our study. A few groups dissolved, most when habitat of their territory was destroyed. Adults predominated among birds moving from one group to another; neither sex predominated. Breeders that disappeared were replaced more often by immigrants than by group members.

All group members assisted in feeding and defending nests, fledglings, and territories. Most helpers were offspring of one or both breeders. Male breeders accounted for the majority of the feeding visits, followed by female breeders and yearling helpers. Individual birds did not account for an increased percentage of feeding visits as they matured. A group attempted no more than one successful nesting and produced an average of 2.3 fledglings per year. Major losses of eggs were through predation (15 of 99) and infertility (21 of 84). Predation was the principal source of nestling loss (25–33 of 40 lost, of 101 total). Groups with helpers did not realize an increase in annual reproductive success when compared to groups without helpers.

The probability of survival increased with age; adult annual survival rate was at least 70% and probably nearer to 80%. Only one known bird failed to breed after reaching adulthood and at least 29 of 34 adults became breeders.

Breeders incur few costs in allowing helpers to remain on the territory and assist at the nest. They probably benefit from the presence of helpers through increased survival and thus in lifetime reproductive output. Helpers forego breeding and remain on occupied territories because by doing so they have a greater opportunity to survive and ultimately reproduce than if they dispersed into ecologically unsuitable, unoccupied areas. Likely reasons that helpers help are that such behavior (1) is a form of payment to the breeders for allowing them access to territorial resources, (2) results in the gain of future help of the young they help raise, and (3) increases their indirect fitness because they help close kin. Any combination of these reasons may be operative.

The social organization and demography of Beechey Jays are remarkably similar to those of Florida Scrub Jays but we found no evidence of the territorial expansion and budding characteristic of Florida Scrub Jays or of specialized dispersal mechanisms as in that species and Green Woodhoopoes. These differences may be related to differences in habitat. Similarly, variation in habitat seems to underlie the considerable differences in social organization between the Beechey Jay and its relatives in *Cissilopha*.

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Appendix

Histories of Beechey Jay Nesting Groups from 1974–1978[a]

Group	Bird (sex)	1974	1975	1976	1977	1978
A	WO (♂)	X, Ad, Np	B, NP	NP	NP	1[b]
	VR (♀)	X, Ad, NP	B, NP	NP	NP	—
	AB	—	B, Yr, H	—	—	—
	GA	—	B, Fl	H	H	—
	BA	—	—	B, Fl	H	—
	GR	—	—	B, Fl	H	—
	VP	—	—	B, Fl	H	—
	OA	—	—	2, H	—	—
B	WV (♂)	B, Ad, NP	NP	NP	NP	NP
	PP (♀)	B, Ad, NP	NP	—	—	—
	AA (♀)	B, Ad, H	3	—	—	—
	GG	B, Yr, H	H	—	—	—
	OG	—	B, Yr, H	H	—	—
	PV (♀)	—	B, Yr, H	H	H	NP
	GV	—	B, Fl	H	H	—
	O/WR (♀)	—	—	X, Ad, NP	B, NP	—
	O/Ar	—	—	—	B, Yr, H	H
	XX	—	—	—	Yr, H	H
	G/Rr	—	—	—	B, Fl	H
	G/Or	—	—	—	B, Fl	H
C	VV (♂)	B, Ad, NP	—	—	—	—
	BR (♀)	B, Ad, NP	NP	NP	NP	NP
	OA	B, 2y, H	2	—	—	—
	OO (♂)	—	4, NP	NP	NP	—
	AV	—	—	B, Fl	H	—
	RV (♂)	—	—	5, H	H	NP
	XX	—	—	—	Yr, H	—
	XX	—	—	—	—	Ad, H
D	OO (♂)	B, Ad, NP	4	—	—	—
	WW (♀)	B, Ad, NP	—	—	—	—
E	RR (♂)	—	X, Ad, NP	B, NP	NP	NP
	AA (♀)	—	3, NP	—	—	—
	XX (♀)	—	Ad, H	NP	NP	NP
	XX	—	Yr, H	—	—	—
	BG	—	—	B, Fl	H	—
	PB	—	—	B, Fl	H	H
	A/Gr	—	—	—	B, Fl	H
F	GB (♂)	X, Ad, NP	B, NP	—	—	—
	OP (♀)	B, Ad, NP	NP	NP	—	—
	WA	—	B, Fl	H	—	—
	RG (♀)	—	—	B, Ad, H	NP	—
	OB (♂)	—	—	6, NP	NP	7
	VG	—	—	8, H	—	—

Appendix
Continued.

Group	Bird (sex)	1974	1975	1976	1977	1978
G	OB (♂)	—	B, Ad, NP	6	—	—
	AP (♀)	—	B, Ad, NP	—	—	—
	XX	—	Ad, H	—	—	—
	XX	—	Yr, H	—	—	—
	XX	—	Yr, H	—	—	—
	RV (♂)	—	B, Fl	5	—	—
	VG	—	B, Fl	8	—	—
H	GO (♂)	—	B, Ad, NP	NP	NP	—
	GV (♀)	—	X, Ad, NP	B, NP	NP	—
	VA	—	B, Yr, H	H	H	—
	XX	—	Yr, H	—	—	—
	P/B	—	—	B, Ad, H	H	—
I	AW (♂)	—	—	B, Ad, NP	NP	—
	XX (♀)	—	—	Ad, NP	NP	—
	RA (♂)	—	—	B, Ad, H	H	—
	AO	—	—	B, Fl	H	1
J	XX (♂)	—	—	Ad, NP	NP	NP
	OW (♀)	—	—	B, Ad, NP	NP	NP
	AR (♂)	—	—	B, 2y, H	H	H
	XX	—	—	Yr, H	H	—
	VW	—	—	B, Fl	H	—
	V/Or	—	—	—	B, Fl	H
	G/Wr	—	—	—	B, Fl	H
K	XX	—	—	—	Ad, NP	9
	V/Gl	—	—	—	B, Ad, NP	—
	XX	—	—	—	Yr, H	—
	A/Gl	—	—	—	B, Yr, H	9
	W/Vl	—	—	—	B, Fl	9
L	XX	—	—	—	Ad, NP	—
	XX (♀)	—	—	—	Ad, NP	NP
	B/Pl	—	—	—	B, Yr, H	H
	W/Bl	—	—	—	B, Fl	H
	G/Al	—	—	—	B, Fl	H
	OB (♂)	—	—	—	—	7, NP

[a] Birds are originally listed in the group and year in which they first appeared. — indicates that the bird disappeared and was presumed dead, fledglings that failed to survive to at least one-year-of-age are not included: X—unbanded, presumed to be the same bird banded in a subsequent year; B—banded; Ad—adult (≥3 years of age); 2y—two-year-old; Yr—yearling; Fl—fledgling; NP—member of nucleus pair (= breeder); H—helper.

[b] Numbers indicate as follows: 1—Observed on study site, but group had dissolved; 2—Absent from study site in 1975, appeared in group A (from group C) in 1976; 3—Moved to group E, from group B; 4—Moved to group C, from group D; 5—Moved to group C, from group G; 6—Moved to group F, from group G; 7—Moved to group L, from group F; 8—Moved to group F, from group G; 9—No nest found, but group presumed present and active on study site.

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A LONG-TERM BIRD POPULATION STUDY IN AN APPALACHIAN SPRUCE FOREST

GEORGE A. HALL

Many studies have shown the relationships between changes in habitat due to plant succession and maturation and the corresponding changes in bird populations, but few of these investigations have been made in the same study area with repeated observations of both bird population and plant succession over a long period of years. Such studies have usually been completed in 1 or 2 years using several nearby areas in different stages of plant succession. These studies have been useful and instructive, but due to yearly population fluctuations such short-term studies may not be truly representative of existing conditions. The use of different areas for the different stages of succession is subject to error of interpretation.

Most of the few long-term studies which have been carried out were made in either nearly mature stands or in greatly disturbed habitats (e.g., city parks) and practically all of them have been done in some type of deciduous forest (see e.g., Kendeigh 1982 and Williams 1947). A long-term study of a hemlock-hardwoods forest using three areas representing three stages of succession in the southern Appalachians in which the areas were censused three times over a 25-year period has been reported (Holt 1974).

In this paper I present the results of population measurements made over a 36-year period, including 22 consecutive years, on a single area of second-growth red spruce forest in the southern Appalachians. The trees grew markedly during this time; bird species composition showed little change, although the populations of most species did change.

THE STUDY AREA

This study was carried out in a large tract of second-growth red spruce (*Picea rubens*) located on Gaudineer Knob, a high point on Shaver's Mountain on the boundary between Randolph and Pocahontas counties, West Virginia. The knob is relatively flat throughout the study area; the summit elevation is 1335 m. Prior to the present century this mountain top was covered with an almost pure stand of mature red spruce. Downslope from the summit the spruce forest changed to a northern hardwoods forest with a broad belt of mixed forest between the two. Sometime between 1905 and 1915 the study area was logged and may have been lightly burned (U.S.F.S. files). Soon after this cutting a second-growth stand of spruce was naturally seeded from the uncut forest nearby. The

FIG. 1. Gaudineer Knob study area and Fire Tower, June 1948.

result has been a dense, almost pure, stand of spruce which forms an effective island surrounded by a nearly pure hardwoods forest. A spruce tree which fell in 1973 had a ring count of just over 50, indicating germination of the seed sometime between 1915 and 1920.

In the 1930s the U.S. Forest Service built a fire-tower at the summit and opened the Knob to visitors by means of the access road. This narrow forest road terminates in a small parking lot at the tower. A few small picnic sites had been opened in the dense forest prior to the beginning of this study. After several years of disuse the tower was removed in 1982.

Ornithologists have been visiting the area since about 1937, at which time the spruce trees were about shoulder-high. There were then a few shrubs mixed with the spruce in a dense stand. Except on the road and a few trails, movement through the area was extremely difficult. At that time the Chestnut-sided and Mourning warblers and the Rufous-sided Towhee were the most common bird species present. (Scientific names of birds are given in the Appendix.)

In 1947 Stewart and Aldrich (1949:7) made a census of the bird population. They described the area as follows; "Vegetation: Dense young spruce averaging about 15 feet in height. Red spruce makes up more than 95% of the trees, the remainder being yellow birch (*Betula lutea*) and mountain ash (*Sorbus americana*). Dense understory of mountain laurel (*Kalmia latifolia*) and a few scattered patches of rhododendron (*Rhododendron maximum*)." At that time a few paths made it possible to move

FIG. 2. Gaudineer Knob study area and Fire Tower, June 1978.

somewhat freely through the Christmas-tree-sized spruces. Figure 1 shows the edge of the parking lot and the tower as they were in 1948.

By the early 1980s the trees were 10—15 m high and ranged from 10—30 cm in diameter. As the crowns of the spruce trees coalesced the understory was crowded out and except along the road and trails the stand has now become pure spruce. The ground is covered only with an accumulation of dead needles and in places, a carpet of mosses. The maximum density of spruce foliage at the level of the understory occurred in about 1958–1960. Since that time the lower branches of the trees have died and at ground level the forest has opened up, although passage through the area is still difficult. There is still no understory, but numerous dead spruce, laurel, and rhododendron stubs remain. During the severe winter of 1976–77 the tops and outer branches of many trees were winter-killed but by 1983 this was no longer evident. Phillips (1979) gives a detailed description of the tract as it was in 1978. Figure 2 shows the parking lot and tower as they appeared in 1978.

TABLE 1
WITHIN-YEAR VARIATION IN NUMBER OF SINGING MALES DETERMINED BY THE INDEX METHOD

Species[a]	1973		1978		1983	
Magnolia Warbler	4[b]	4[c]	5[d]	3[e]	2[f]	2[g]
Dark-eyed Junco	10	8	8	8	9	7
Swainson's Thrush	2	1	2	1	1	2
Golden-crowned Kinglet	3	2	4	2	5	4
American Robin	2	2	2	1	2	2
Winter Wren	1	2	—	—	2	2
Hermit Thrush	1	1	1	1	3	2
Black-capped Chickadee	—	1	—	1	—	—
Blue Jay	—	—	—	1	—	—
Yellow-rumped Warbler	—	—	2	3	1	2
Black-throated Green Warbler	—	1	—	—	—	—
Solitary Vireo	—	1	—	—	—	—
Black-throated Blue Warbler	—	—	—	1	—	—
Totals	23	22	24	22	25	23

[a] See Appendix for scientific names.
[b] = June 1.
[c] = June 11.
[d] = May 30.
[e] = June 6.
[f] = May 30.
[g] = June 11.

CENSUSING METHODS

The census area is a 6.08-ha rectangular plot (100.6 m × 803.6 m) centered on the road and one of the narrow trails. This area was censused by the spot map method (Hall 1964) in 1947 (Stewart and Aldrich 1949). In 1948 the members of the Brooks Bird Club began a series of censuses by the spot-mapping method made in early June, which have continued to the present at 5-year intervals (DeGarmo 1948, 1953; Hall 1958; Hurley 1964; Koch 1968; DeGarmo and Koch 1974; Phillips 1979, 1984).

In 1959 a program of annual censuses by a rather different "index method" was begun. The method adopted has the merit of giving a satisfactory index of the number of territorial males in a minimum amount of time—one overnight trip to the area.

The index method consists of traversing the length of the study area in a fairly rapid fashion, tallying all the birds seen and heard during the traverse. This traverse requires about 12 min to complete. After a wait of about 3 min the area is traversed in the reverse direction. This down-and-back procedure is then repeated giving four traverses of the same route. One set of four is made during the last hour before dark (approximately 19:45–20:45 EDT) and another set of four is made in the first hour of daylight the next morning (05:30–06:30). After the evening counts a tentative judgment is made as to the probable number of singing males of each species on the area, and at the end of the morning counts final judgment of the population is made. Counts of this nature have been made in the last 2

TABLE 2

SINGING MALE NUMBERS DETERMINED BY THE SPOT-MAPPING METHOD

Species*	1947	1948	1953	1958	1964	1968	1973	1978	1983
Magnolia Warbler	15	19	19	11	9	8	1.5	1	2.5
Dark-eyed Junco	8	10	8	4.5	6	10	6	8	5
Swainson's Thrush	6	2.5	6.5	5.5	3.5	1	0.5	1	—
Golden-crowned Kinglet	—	—	1	0.5	2	2	5	3	5
American Robin	2	4.5	4.5	3	1	3	2	1	1.5
Winter Wren	2	2	2	0.5	1.5	2	1	—	—
Hermit Thrush	0.5	—	1.5	—	—	0.5	—	—	—
Black-capped Chickadee	0.5	1	2	—	—	1.5	1	—	—
Blue Jay	—	—	—	—	—	2	1	—	—
Northern Waterthrush	—	—	3	1.5	1.5	—	—	—	—
Yellow-rumped Warbler	—	—	—	—	—	—	—	2	2.5
Rufous-sided Towhee	5	5.5	4	—	—	—	—	—	—
Black-throated Green Warbler	0.5	—	—	—	0.5	—	—	—	0.5
Blackburnian Warbler	—	0.5	—	—	—	0.5	—	—	—
Solitary Vireo	—	—	—	—	—	—	0.5	—	0.5
Veery	0.5	—	1.5	—	—	—	—	—	—
Black-throated Blue Warbler	—	3.5	0.5	—	—	—	—	—	—
Chestnut-sided Warbler	1	0.5	—	—	—	—	—	—	—
Purple Finch	1	1	1	0.5	—	0.5	—	—	—
Cedar Waxwing	—	1	—	—	—	—	—	—	—
Canada Warbler	—	0.5	1	—	—	—	—	—	—
Red-eyed Vireo	—	—	—	—	—	—	0.5	—	—
Species	12	13	14	8	8	12	10	6	7
Total (males)	42	51.5	55.5	27	25	31	19	16	17.5

* See Appendix for scientific names.

days of May or the first 2 days of June from 1959 through 1983. All counts through the years were made by the same observer. In the early years the index method counts were not too reliable while the method was being worked out, but with added experience the later counts have been good measures of the population. In 1973, 1978, and 1983 an additional index method count was made later in June to give some idea of the variation expected by this method. This comparison is given in Table 1. It is noted that most of the rarer species agree exactly but that some of the more numerous species differ by ± 1 male, and the total population varies by ± 2 males. In 1983 this variation in the Yellow-rumped Warbler and the Swainson's Thrush may have been due to the arrival of late migrants. In 1964, 1968, 1973, 1978, and 1983 it was possible to compare the index method results with those of the more conventional spot-mapping method (see Tables 2, 3, 4). For species with small populations the two methods agree quite well, but for the abundant species the index method appears to overestimate the population. This happens because this method makes no allowances for the fractions of certain territories being outside the boundaries of the study area. The difference is slight for individual species but the accumulated error in the total population is sometimes large. In 1983, when allowances were made for this effect, the

TABLE 3

SINGING MALE NUMBERS DETERMINED BY THE INDEX METHOD 1962–1972

Species*	1962	63	64	65	66	67	68	69	70	71	72
Magnolia Warbler	12	11	10	10	10	5	10	8	9	9	10
Dark-eyed Junco	3	4	5	7	7	7	7	7	10	10	9
Swainson's Thrush	3	4	4	4	3	2	2	2	2	2	3
Golden-crowned Kinglet	1	1	3	2	3	3	3	2	2	2	2
American Robin	—	3	1	3	3	3	3	2	3	3	3
Winter Wren	—	2	1	2	1	2	—	1	—	1	1
Hermit Thrush	1	2	—	—	1	—	—	1	—	2	2
Black-capped Chickadee	—	—	1	1	2	2	4	2	3	2	2
Blue Jay	—	2	—	1	1	2	2	—	1	1	1
Northern Waterthrush	3	4	3	2	2	3	3	—	2	—	1
Yellow-rumped Warbler	—	—	—	—	—	—	—	—	—	—	—
Rufous-sided Towhee	—	—	—	2	—	—	2	1	3	1	2
Black-throated Green Warbler	1	—	3	—	1	—	—	—	—	—	—
Blackburnian Warbler	—	—	—	1	1	—	—	—	—	—	—
Solitary Vireo	—	—	—	—	—	—	—	—	1	—	—
Wood Thrush	—	—	—	—	1	—	—	—	—	—	—
Veery	—	—	—	—	—	—	—	—	—	1	—
Black-throated Blue Warbler	1	—	—	—	1	—	—	—	—	—	—
Chestnut-sided Warbler	1	—	—	—	—	—	—	—	—	—	—
Purple Finch	—	—	—	—	—	—	—	—	—	—	—
Species	9	9	9	11	14	9	9	9	10	11	11
Total (males)	26	33	31	35	37	29	36	26	36	34	36

* See Appendix for scientific names.

population estimates agreed almost exactly. The accuracy of the index method is highly sensitive to the weather. Inclement weather on the one day selected for the count can cause large errors. This is the apparent cause of the low count for 1967, made in a cold drizzle on the only 2-day period available that season.

RESULTS

The results of the nine singing-male censuses are given in Table 2 and those for the 22 most recent index counts are given in Tables 3 and 4. These data are also plotted in Figs. 3 and 4.

Over the 35-year period the general species composition has remained the same, although the number of species decreased markedly during the period 1953–1958. This decrease resulted from the elimination of some marginal species such as the Chestnut-sided Warbler, Purple Finch, and Rufous-sided Towhee, rather than any change in the most numerous species. The population also declined during this period. This decline resulted largely from the decrease in Magnolia Warblers which had been

TABLE 4

SINGING MALE NUMBERS DETERMINED BY THE INDEX METHOD, 1973–1983

Species*	1973	74	75	76	77	78	79	80	81	82	83
Magnolia Warbler	4	8	9	5	4	3	3	2	3	3	2
Dark-eyed Junco	9	8	11	11	9	8	8	11	11	9	8
Swainson's Thrush	2	2	2	2	3	2	2	2	2	3	2
Golden-crowned Kinglet	3	5	4	6	3	4	4	5	5	5	5
American Robin	2	3	2	2	1	2	2	1	—	2	2
Winter Wren	1	—	2	2	1	—	2	1	1	3	2
Hermit Thrush	1	3	1	2	—	1	2	2	3	3	3
Black-capped Chickadee	1	—	3	—	2	—	1	1	—	—	—
Blue Jay	—	1	—	1	—	1	1	—	—	—	—
Northern Waterthrush	2	—	—	—	—	—	—	—	—	—	—
Yellow-rumped Warbler	—	—	1	1	1	2	1	1	3	3	3
Rufous-sided Towhee	—	—	—	—	—	—	1	—	—	1	—
Black-throated Green Warbler	—	1	—	—	—	—	1	—	—	—	—
Blackburnian Warbler	—	1	1	—	1	—	—	—	—	—	—
Solitary Vireo	1	—	1	—	—	—	1	—	—	—	—
Wood Thrush	—	—	—	—	—	—	—	—	—	—	—
Veery	—	—	—	—	—	—	—	—	—	—	—
Black-throated Blue Warbler	—	—	—	—	—	—	—	—	—	—	—
Chestnut-sided Warbler	—	—	—	—	—	—	—	—	—	—	—
Purple Finch	—	1	—	—	—	—	—	—	—	—	—
Species	10	10	11	9	9	8	13	9	7	9	8
Total (males)	26	33	37	32	25	23	29	26	28	32	27

* See Appendix for scientific names.

the most abundant species. The population of the other important species, the Dark-eyed Junco, remained essentially constant, although there were small year-to-year fluctuations. After this initial decline the total population has remained almost constant. Since 1963 there has been a slight, but statistically significant decrease ($r = 0.503$, $P = 0.02$), but since 1976 the total population has remained constant within the normal error of the counts. The Magnolia Warbler population has continued to decline, but this decrease has been made up by the increase in Yellow-rumped Warbler and Golden-crowned Kinglet populations.

DISCUSSION

The major change in population between 1953 and 1958, which resulted largely from the decline of Magnolia Warblers, coincided with the time at which the canopies of the young spruce trees coalesced, eliminating all other plant species. At this time the niche for ground-inhabiting birds was eliminated and these species, along with those requiring some plants

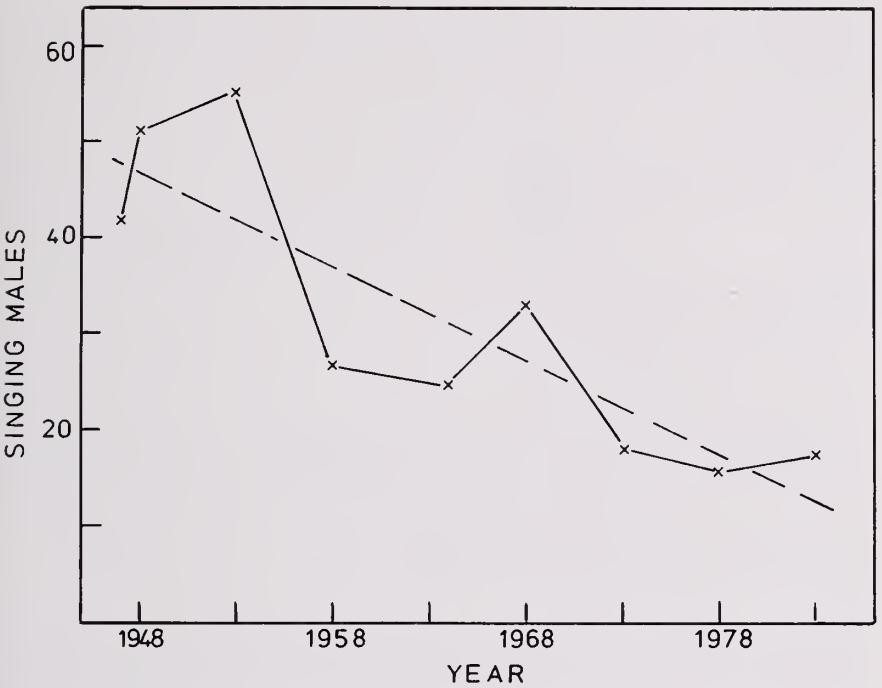

FIG. 3. Total number of singing males as determined by the spot-mapping method. (For the regression line $R = -0.862$, $df = 7$, $0.001 < P < 0.01$.)

besides spruce, disappeared. The lack of openings in the spruce was apparently unfavorable for the Magnolia Warbler whose numbers declined, although at this time it was still the most numerous species on the area. Morse (1968) has shown that this species forages mostly on the outer tips of conifer branches. The spire-like form of the young spruce trees assures that outer tips of branches will always be available in the open as the trees grow, although these will be at increasing heights.

Since 1958 the Magnolia Warbler population has continued to decline slowly. This may be related to the continued growth of the trees, but in mature habitats on this mountain, where plant growth is not as marked a factor, the populations of this species (which were never as large as the ones in the study area) have also declined (Hall 1984). The general decrease may be related to the possible continent-wide decline of Neotropical migrants (Criswell 1975, Terborgh 1980, Hall 1984).

The singing-male censuses taken at 5-year intervals also showed an abrupt drop in Magnolia Warbler populations between 1968 and 1973.

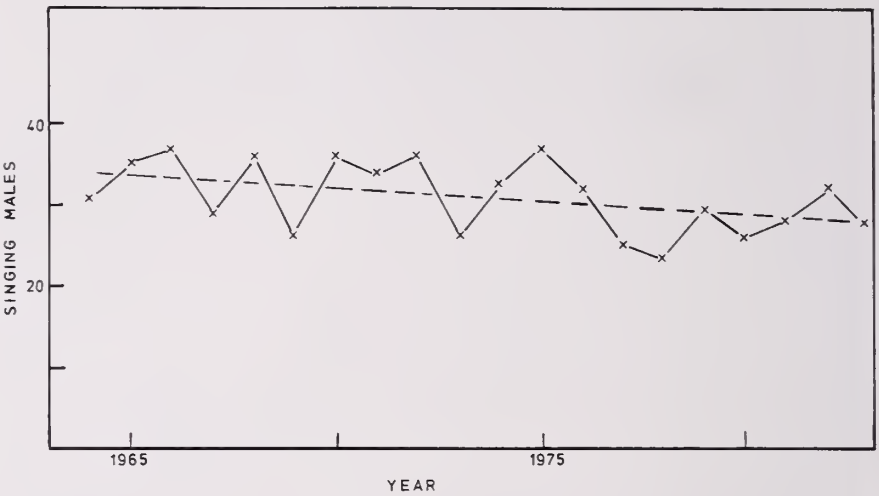

FIG. 4. Total number of singing males as determined by the index method. (For the regression line $R = -0.503$, $df = 19$, $P = 0.02$.)

If only these 5-year counts were available this drop might not seem unexpected but the yearly censuses show that this decrease took place all in 1 year, an event not to be expected. It seems likely that the low 1973 counts were produced by the conditions that prevailed when Hurricane Agnes moved through the eastern states in June 1972. As a result of this disturbance, which produced heavy flooding to the east and northeast of the study area, the mountain experienced fog with rain (and perhaps some snow) and abnormally low temperatures for perhaps 10 days. This occurred at a critical time in the nesting cycle and it is reasonable to assume that practically no Magnolia Warbler nestlings survived. All warbler species were in lower than normal numbers in these mountains in 1973. The population did return to a higher value in 1974, although the overall decline has continued.

The other common species, the Dark-eyed Junco, has shown an essentially stable population over the years, possibly with a small increase. This species is now nesting in the lower branches of the trees since most of the more usual ground-nesting sites have been eliminated. Juncos will nest several times during the summer, and so the breeding season of 1972 was not so disasterous for them as it was for the Magnolia Warbler. As the lower branches of the spruce disappear we might expect an eventual decline in junco populations also, but this is not evident as yet.

When the trees reached a sufficient height the Golden-crowned Kinglet

invaded the area. For about 10 years the kinglet population remained fairly constant and then the numbers increased markedly. This increase in population was not peculiar to this area but took place throughout the southern part of its range. The population of kinglets, both on this study area and in this general region, crashed suddenly in 1977. This was presumably due to a large winter-kill in late winter of 1977 when abnormally cold temperatures extended far into the winter range of this kinglet. Since 1977 the population has been building up again.

Swainson's Thrushes, which were one of the more common species in the early years, had a major decline in numbers at about the time the canopies coalesced, but have had an essentially constant population since about 1967. The Hermit Thrush has never been common on this tract, being more characteristic of the mixed hardwoods-spruce forest on the mountain side. In recent years Hermit Thrushes have appeared on the study area, and have shown a small increase in population. This increase may have resulted from the decline in Swainson's Thrushes which often displace Hermit Thrushes in this spruce forest (Hall 1983).

The Northern Waterthrush was first found on the area in 1953 and it remained, in essentially stable numbers, for 23 years and then disappeared. This appears to be a good example of a colonization of an area followed by ultimate extirpation. This mountaintop, far from any standing water, seems an unlikely place for this species, but it might be postulated that it is wet vegetation, or wet ground cover, and not water as such, that this species requires. During the breeding season this spruce forest is usually quite wet from the heavy rains which are characteristic of that season. The disappearance of the waterthrush coincided with the elimination of the lower branches of the spruce trees and the opening up of the forest floor.

Another example of a colonization is that of the Yellow-rumped Warbler. This species had not been known to nest south of northeastern Pennsylvania before 1975 when it appeared during the breeding season on this study area. Since that time the population has increased modestly, and the species has now been found in summer elsewhere in the West Virginia spruce forest. It will be of interest to follow this species to see if colonization will be successful or if, like the waterthrush, the Yellow-rumped Warbler will ultimately disappear.

The occasional appearance of Black-throated Green and Blackburnian warblers in this young spruce forest presents an interesting strategy by which a new species may arrive on an area. Both of these species should ultimately occupy this area when the trees reach adequate size, although the Black-throated Green Warbler may require more deciduous growth than is present here. Apparently from time to time pioneers enter the area

and attempt to breed in a habitat that is not quite suitable for them. The nesting is unsuccessful and the species is missing from the area until another pioneer makes the attempt. Eventually the habitat may become suitable and the species becomes established.

That this area has shown so little change in species composition over the years is apparently characteristic of the northern coniferous forest. A nearby area of deciduous growth at much the same elevation censused for the first time in 1947 (Stewart and Aldrich 1949) has shown a great change in species composition, and in population in this intervening time (see Phillips 1974).

Schreiber and Schreiber (in press) have recently pointed out that the effects of the Pacific Ocean phenomenon known as the Southern Oscillation (El Niño) may have far-reaching effects on bird populations even well away from the Pacific area. It is intriguing to note that the low populations in 1958, 1964, and 1973 were El Niño years, but so too was 1953, when the population was unusually high. No conclusions are to be drawn but the subject deserves thought.

The population of an area in a boreal forest at any particular time is highly dependent not only on climatic factors, but also on short-term weather factors. Thus, the 1973 values on this area are greatly influenced by the unfavorable weather events of the previous summer and are not representative of the long-term trends on the area. There is some evidence (Hall 1984) that there may be no "equilibrium" population in the mature boreal forest.

While the number of species on the area never exceeded 14 in any one year, 23 species have been listed over the years. Examination of the tables shows that many species fluctuate between being present and being absent. Such fluctuations lead to high rates of turnover in species presence. The average annual turnover rate on this plot is 22.8% (9.1–40.0%); the overall turnover rate is much higher. The present study area can be considered as being representative of an island of spruce forest in a sea of different habitat, and turnover rates of islands calculated on the basis of yearly counts are typically high (Diamond and May 1977). These turnover rates are somewhat higher than those reported from yearly counts on the California Channel Islands (Jones and Diamond 1976). The relatively small size of this study plot may serve to artifically exaggerate the turnover rate.

Much of ecological theory is derived from censuses made in only one year, but as the 1973 data given above show, the conclusions drawn from such "one-shot" counts may well be misleading. The index method used here is also a "one-shot" procedure for any given year and hence may be in error for that year, but over many years the effects of unusual conditions in any one count will be offset. Thus, as noted above, the 1967 count is probably highly unreliable.

In order to make valid ecological generalizations bird populations should be measured over a period of several years. Unfortunately, this is often not practical. Even more unfortunately, however, the limitations of a 1 or 2 year study are often not recognized.

SUMMARY

The breeding bird population in a stand of second growth red spruce forest in eastern West Virginia was determined at 5-year intervals by the spot-mapping method from 1947–1983. From 1962–1983 the population was also monitored annually by a somewhat cruder "index method." In these 36 years the overall species composition changed very little, although the number of species and the total number of males underwent a marked reduction at about the same time the crowns of the spruce trees coalesced and eliminated all other plant species from the area. Since that time the population has remained essentially constant, although a slow decline appears to be taking place.

In boreal habitats such as this one the population determined in any one year is very sensitive to weather factors. Possible fluctuations due to such factors must be considered in drawing ecological conclusions from data obtained in a single year.

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APPENDIX
SCIENTIFIC NAMES OF BIRDS

Blue Jay (*Cyanocitta cristata*)
Black-capped Chickadee (*Parus atricapillus*)
Winter Wren (*Troglodytes troglodytes*)
Golden-crowned Kinglet (*Regulus satrapa*)
Veery (*Catharus fuscescens*)
Swainson's Thrush (*Catharus ustulatus*)
Hermit Thrush (*Catharus guttatus*)
Wood Thrush (*Hylocichla mustelina*)
American Robin (*Turdus migratorius*)
Cedar Waxwing (*Bombycilla cedrorum*)
Solitary Vireo (*Vireo solitarius*)
Red-eyed Vireo (*Vireo olivaceus*)
Chestnut-sided Warbler (*Dendroica pensylvanica*)
Magnolia Warbler (*Dendroica magnolia*)
Black-throated Blue Warbler (*Dendroica caerulescens*)
Yellow-rumped Warbler (*Dendroica coronata*)
Black-throated Green Warbler (*Dendroica virens*)
Blackburnian Warbler (*Dendroica fusca*)
Northern Waterthrush (*Seiurus noveboracensis*)
Mourning Warbler (*Oporornis philadelphia*)
Canada Warbler (*Wilsonia canadensis*)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)
Dark-eyed Junco (*Junco hyemalis*)
Purple Finch (*Carpodacus purpureus*)

Wilson Bull., 96(2), 1984, pp. 241–248

REPRODUCTION BY JUVENILE COMMON GROUND DOVES IN SOUTH TEXAS

MICHAEL F. PASSMORE

Breeding at less than 10–12 months of age is rare among birds (Skutch 1976). Most species breeding in their first calendar year are passerines (Miller 1955, 1959) or domesticated forms (Esner 1960, Johnston 1962). Stubble Quail (*Coturnix novaezealandiae*) and Japanese Quail (*C. coturnix*) can breed when 4 months old if environmental conditions are favorable (Disney 1978).

Reproduction by juveniles has been reported for several species of Columbiformes. Irby and Blankenship (1966) reported nesting by juvenile Mourning Doves (*Zenaida macroura*) in Arizona. Precocial testicular development has been found in juvenile Mourning Doves as far north as Ontario (Armstrong and Noakes 1977). Murton et al. (1974) noted that Eared Doves (*Z. auriculata*) were able to breed in captivity at 4–5 months of age; apparently, many wild juveniles of that species bred during their first year. Evidence of breeding by a juvenile Common Ground Dove (*Columbina passerina*) was described by Johnston (1962). The objective of my study was to determine both the extent of juvenile reproductive activity in a wild population of Common Ground Doves, and the significance of this phenomenon for the annual reproductive output of the population.

STUDY AREA AND METHODS

Reproduction in juvenile ground doves was studied during May 1978 through October 1980 on two cattle ranches near Dinero, Live Oak Co., Texas. The Twin Oaks Ranch (TOR) encompassed nearly 8100 ha, situated along the western edge of Lake Corpus Christi.

My main study area on the TOR was in an 810-ha pasture, 2 km northwest of Lagarto, Texas. Most of the pasture had recently been aerially sprayed for control of mesquite (*Prosopis glandulosa*) which created an abundance of dead-snag mesquites surrounded by dense clumps of shrubs (mainly agarito [*Berberis trifoliolata*], *Lantana* sp., and blackbrush [*Acacia rigidula*]). Periodic shredding of low brush on the sandy soil stimulated excellent growth of annual grasses and forbs which supported an abundance of doves.

The second study area was on the 1200-ha C. N. Freeman Ranch, 3 km north of Dinero. This area was mainly rolling hills covered by mesquite, live oak (*Quercus virginiana*), and chaparral. Chaparral species were mainly blackbrush, colima (*Zanthoxylum fagara*), and ceniza (*Leucophyllum frutescens*). Approximately 80% of the brushland on the ranch had recently been chained; most of the cleared land was converted to coastal Bermuda grass (*Cynodon dactylon*).

Ground doves were mainly collected by mist nets set near feeding areas or stock tanks; a few birds were collected by shooting. Sacrificed ground doves were placed in a portable cooler to minimize dessication. Within 12 h of collection (most within 1–4 h), gonads were removed from the body cavity and measured with Vernier calipers to the nearest 0.1 mm.

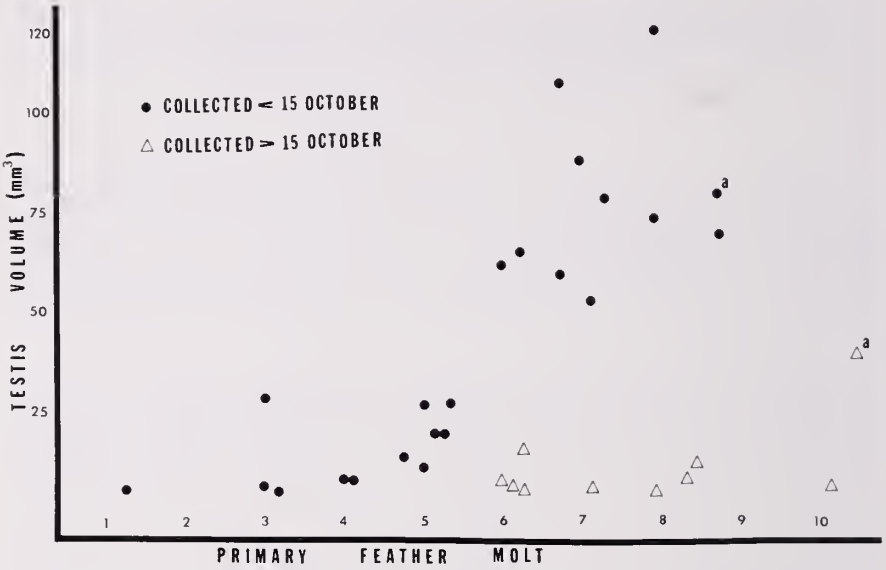

FIG. 1. Relation of testicular volume (mm^3) to the stage of primary feather molt of juvenile ground doves collected during April–15 October and 16 October–December 1978–1980 in Live Oak County, Texas. Primary molt stage represents the percent of replacement for each primary, i.e., molt stage 7.5 indicates P-7 was one-half replaced. a = juveniles with active crop milk glands.

Diameter of the largest ovarian follicle was recorded for females. For males the length and width of the left testis was recorded. Testicular volume was estimated using $V = 4/3\ W^2\ L$, where V = volume, W = ½ width, and L = ½ length (Lofts and Murton 1966, Gutierrez et al. 1975). Crop glands were classed as active (producing crop milk) which included developing and regressing stages, and inactive (Zeigler 1971). Additionally, ovaries were macroscopically examined for evidence of ovulated follicles. Ovulated follicles appeared as flaccid, dark follicle membranes within the ovary.

Juveniles were identified by the presence of white-tipped upper wing coverts, white-tipped allulars, and a Bursa of Fabricius. Molt discussed herein refers to the loss of a feather, and undifferentiated follicles refer to ovarian follicles of approximately the same granular size (<1 mm).

RESULTS

Gonadal activity.—A total of 74 juvenile ground doves were sacrificed during the 3-year period. Of those, 71 (33 male, 38 female) provided paired measurements of primary feather molt and gonadal sizes.

Testicular enlargement in juvenile males began concurrently with the molt of their fifth primary (P-5) (Fig. 1). All juvenile males that had molted at least P-6 and were taken prior to 15 October (N = 11), had

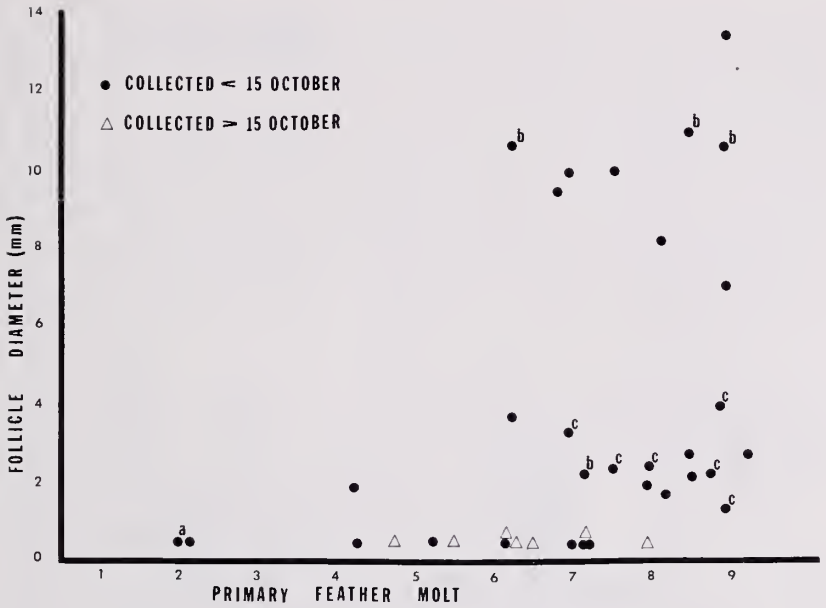

FIG. 2. Relation of the diameter of the largest follicles (mm) to the stage of primary feather molt of juvenile ground doves collected during April–15 October and 16 October–December 1978–1980 in Live Oak County, Texas. Primary molt stage represents the percent of replacement for each primary, i.e., molt stage 7.5 indicates P-7 was one-half replaced. a = undifferentiated ovary assigned a value of 0.5 mm; b = partially shelled egg present in oviduct; c = active crop gland.

testicular volumes greater than 50 mm^3. One juvenile that had molted P-3 had a testicular volume of 28 mm^3; a small percentage of juvenile males may therefore become sexually mature earlier than the majority of their cohorts.

The mean testicular volume for adults during the breeding season was 129 mm^3 (range = 73–197 mm^3) (Passmore 1981). Although 7 of 11 juveniles that had molted P-6 had testicular volumes within the adult range, only one had a testicular volume (121 mm^3) near the adult mean. Because no information is available on the minimum testicular volume required for successful breeding in the Common Ground Dove, I could not determine which juvenile males were sexually mature based on gonadal volume.

Regression of testes in juveniles was similar in timing to that of adults. Ten juvenile males that had molted at least P-6 were collected during late October; their mean testicular volume was 9.8 mm^3 (range = 2–39 mm^3).

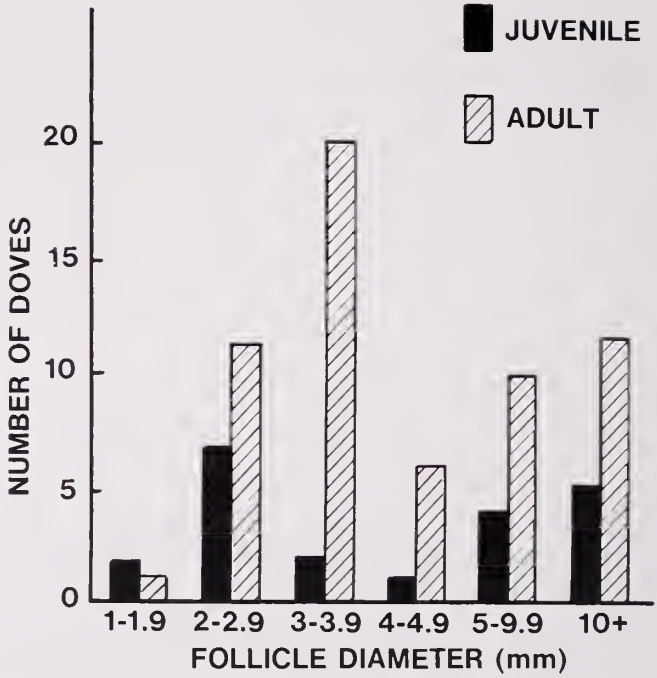

FIG. 3. Frequency distribution of largest follicles in adult and juvenile ground doves collected during 1978–1980 in Live Oak County, Texas.

All seven adult males taken during January and February had testicular volumes less than 10 mm^3.

More direct evidence of breeding was observed in juvenile females. Enlarged ovarian follicles were evident in most (22 of 26) juveniles after P-6 had been molted (Fig. 2). One female that had molted P-4 had an enlarged follicle (1.9 mm), again suggesting that some juveniles become sexually mature at an earlier age than most of the juvenile population. There was a difference ($\chi^2 = 12.9$, df = 5, $P < 0.05$) in the frequency distribution of follicle sizes in adults and juveniles during the breeding season (Fig. 3).

Unlike males, in which all juveniles molting P-6 or more had enlarged testes, 15% (4 of 26) of the females that had molted P-6 or more did not have differentiated follicles. No relationship was found between the lack of gonadal activity in those females and the months in which they were collected.

Nine juvenile females had ovarian follicles larger than 6.0 mm in diameter; I assumed those follicles were enlarging prior to ovulation, based

on the size of the quiescent stage (2.0–4.0 mm) of the follicles (Fig. 2). Three doves with follicles larger than 6.0 mm also had partially shelled eggs in their oviducts. Two with oviducal eggs also had two enlarged follicles (11.0 and 7.0 mm; 10.6 and 8.2 mm) in the ovaries. As the normal clutch-size is two in this dove (Bent 1932; Passmore, unpubl.), those birds with oviducal eggs and two enlarged follicles were apparent anomalies. This physiological phenomenon was not observed in adults. It was possible that enlarged follicles may degenerate following the laying of the second egg. Overall, 89% (33 of 37) of all juveniles (males and females) that had molted P-6 or more prior to mid-October had enlarged gonads.

Crop gland activity.—Presence of active crop glands in ground doves was interpreted as evidence of a successful hatching (Zeigler 1971). One juvenile male collected in August 1979 (P-8 ¾ replaced; $V = 79$ mm^3) had an active crop gland (Fig. 1). Five of 21 juvenile females had active crop glands; the proportion of adult females with active crop glands (14 of 59) was nearly identical ($\chi^2 = <0.01$, $df = 1$, $P > 0.05$).

Four of 11 juvenile females with follicles of 2.0–4.0 mm in diameter (estimated quiescent range) had active crop glands (Fig. 2). One female taken in September 1979 had a follicle of 1.4 mm in diameter and active crop glands. This bird may have terminated its ovarian cycle for the season and was in the refractory stage.

DISCUSSION

A paucity of information exists on the contribution by birds-of-the-year to the annual reproductive output of a population. Brown (1967) suggested that juvenile Mourning Doves in Arizona may effect an increase of 1–4% in the annual production. He estimated that approximately 14% of the juveniles sampled were reproductively mature and that some bred at the age of 90 days.

The contribution by juvenile Common Ground Doves to the annual recruitment of the population appeared to be substantial. A simulation model was developed to estimate this contribution (Fig. 4).

I selected an initial population of 500 pairs of adults (second year or older). The breeding season was estimated to be 24–28 weeks long, based on gonadal patterns of ground doves collected during this study. The time required for egg-laying, incubation, and fledging was estimated to be 28 days. Additionally, there is a period of unknown length between the departure of fledglings and the laying of the next clutch. Skutch (1956) and Haverschmidt (1953) found this period to be 8–31 days for consecutive broods of Ruddy Ground Doves (*Passerina talpicoti*). Thus, ground doves in south Texas may have three successful nestings during the 6–7 month

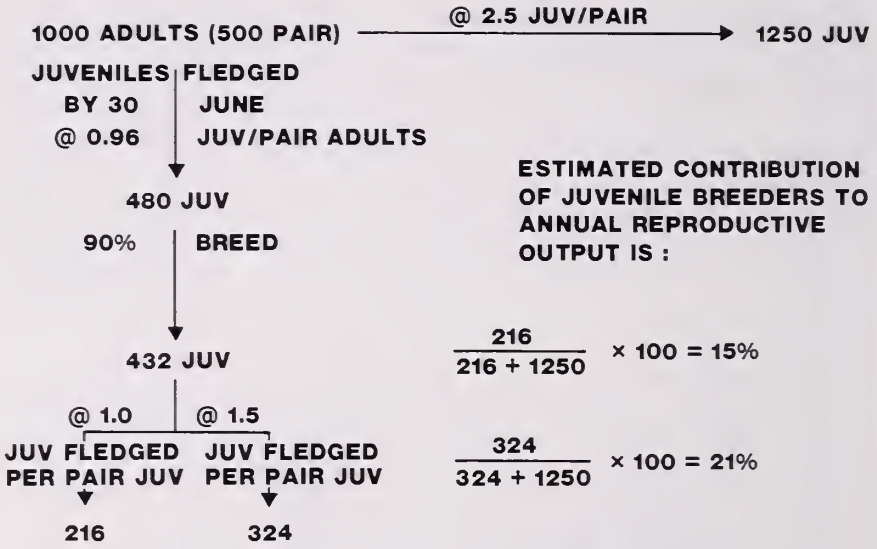

FIG. 4. Simulation model of the contribution of breeding by juvenile ground doves to the annual productivity of a ground dove population. See text for explanation.

breeding season. An annual production rate of 2.5 young per pair of adults represents 42% egg success based on an assumed two eggs per nest. Annual production of the 500 pairs of adults was therefore estimated to be 1250 young.

Without having direct evidence of production from marked or captive pairs of ground doves, I believed 2.5 young per pair to be a realistic estimate. Skutch (1956) reported a 20% egg success of Ruddy Ground Dove nests (two nestings per year). Swank (1955) found Mourning Doves in Texas had approximately 60% nesting success and produced slightly over three young per pair, based on wings collected during the hunting season. Hanson and Kossack (1963), working in an area where Mourning Doves averaged two nestings per year, found production of about 2.4 young per pair.

To estimate the contribution of breeding by juveniles, I first estimated the number of juveniles which had fledged by the end of June. These juveniles would thus be at least 80 days old (most over 100 days) by 1 September; theoretically, all should have an opportunity for at least one breeding attempt. This estimate was based on the mean age ratio (0.46 juveniles/adult, N = 297) of ground doves captured in June of 1978 and 1979.

Based on data previously presented concerning gonadal sizes (Figs. 1, 2), I estimated 90% of those juveniles fledged by the end of June would become sexually active. I assumed all juveniles with enlarged gonads would breed. Two scenarios were envisioned in which the average production per pair of juveniles was arbitrarily selected to be 1.0 or 1.5 young. Those juveniles hatched in April had time to complete two nestings (and thereby produce 1.5 young) by late October. However, birds fledged in June likely were able to complete only one nesting (producing 1.0 young).

Hence, juveniles fledged by 30 June could contribute 216–324 (15–21%) of the annual reproductive capabilities of the hypothetical population (Fig. 4). Further research may substantially refine these estimates depending on behavioral characteristics and reproductive success of juvenile ground doves.

Early sexual maturation in a juvenile ground dove in Florida was reported by Johnston (1962). Johnston collected a juvenile female which had a partially shelled egg in the oviduct and two ovulated follicles. The fifth primary apparently was ¼–½ replaced, indicating to Johnston that the dove's age was between 5 and 6 months. My data indicated that a ground dove with P-5 one-half replaced would be approximately 2.5 months old. I did not observe evidence of breeding prior to the molt of P-6 in juveniles (Figs. 1, 2). A difference may therefore exist in maturation schedules between ground doves (*C. p. pallescens*) in south Texas and those (*C. p. passerina*) in southern Florida.

SUMMARY

Reproductive activity in juvenile Common Ground Doves (*Columbina passerina*) was studied in mesquite-brushland habitats in south Texas from 1978–1980. Juveniles were reproductively active near the time they molted their sixth juvenal primary, at approximately 79 days of age. Evidence of breeding included enlarged testes, differentiated ovaries, active crop glands, and oviducal eggs. The contribution of juvenile breeders to the annual recruitment of the population was estimated to be 15–21%.

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OCCURRENCE OF SUPERNORMAL CLUTCHES IN THE LARIDAE

MICHAEL R. CONOVER

In recent years, female-female pairings have been discovered in Western Gulls (*Larus occidentalis*) (Hunt and Hunt 1977), Ring-billed Gulls (*L. delawarensis*) (Conover et al. 1979, Ryder and Somppi 1979), California Gulls (*L. californicus*) (Conover et al. 1979), and Herring Gulls (*L. argentatus*) (Fitch 1979). These associations occur when two females pair together rather than with male mates and both lay eggs in a mutual nest. It has yet to be determined whether female pairs are restricted to a small number of gull species or are widespread among the normally monogamous Laridae. Supporting the latter possibility is the recent discovery of female pairs among breeding Caspian Terns (*Sterna caspia*) (Conover 1983). Such female pairs are often identifiable because their nests contain supernormal clutches (4–6 eggs), double the normal clutch-size. Not all supernormal clutches (SNCs), however, result from female pairings. In a study of Ring-billed Gulls, 17% of the 5–6 egg clutches resulted from polygynous associations in which two or more females lay eggs in the same nest (Conover, in press). Furthermore, a polygynous group was found attending a SNC in the Brown Skua (*Catharacta skua*) (Bonner 1964). Hence, the presence of SNCs in a particular species may indicate that either female pairings or polygynous associations occur in that species. This is not necessarily the case, however, for a few SNCs may also result from adults rolling a foreign egg into their nest or from nest parasitism although normally neither event should cause a doubling of clutch-size, except for one-egg clutches.

In this study, I used clutch-size data to estimate the frequency of SNCs in different gull and tern species. Such information is useful in identifying those species in which female pairings or polygyny may occur. These data were also used to test the hypothesis that DDT contamination produces female pairings by feminizing male embryos (Fry and Toone 1981). If this is so, the frequency of female pairs and consequently SNCs should have increased since the late 1940s when DDT's widespread usage began.

METHODS

Definition of supernormal clutch.—Supernormal clutch, an imprecise term, has historically signified an unusually large clutch. This term has been applied mostly to birds which usually lay three-egg clutches; for these birds, most authors agree that clutches containing five or more eggs are supernormal but disagree on the inclusion of four-egg clutches. Hunt and

Hunt (1977) and Conover et al. (1979) have included them while Ryder and Somppi (1979) and Shugart (1980) have not. Therefore, a more precise definition is necessary, especially for studies of other species which do not lay a three-egg clutch. Bonner (1964) considered a three-egg clutch to be supernormal in the Brown Skua, a species which lays two eggs.

I use the following definition: a supernormal clutch exceeds the modal clutch-size by more than 50% with the exception that a two-egg clutch shall only be considered supernormal if 90% of the individual females lay a single egg. Hence, if the modal clutch-size contains 2, 3, or 4 eggs, then SNCs must contain at least 4, 5, or 7 eggs, respectively.

Data collection procedures.—Clutch-size data used in this study came from two sources. First, data were gathered from most of the major museum egg collections in North America. For each egg set examined, I recorded the clutch-size, species, year, and collection site. While either I or my technicians examined most egg sets, some additional data were furnished by the staff of museums which I was unable to visit. Data from egg collections represent pre-DDT conditions because few egg sets have been collected since 1940.

The remaining data on clutch-size frequencies for gulls and terns were obtained by literature search. Excluded from this analysis were some reports in which: (1) fewer than 50 nests were sampled in those species where sample sizes were already so large that such studies added little; (2) the number of nests of each clutch-size was not given or was estimated rather than counted directly; (3) nests were not randomly selected or for some were not representative of that species due to some unusual situation (such as studies prompted by an unusual event like birds nesting out of season or after a natural disaster); (4) the count was made either before most of the clutches were completed or after many of the eggs had hatched; or (5) the reliability of the data was uncertain (i.e., misidentified species, mathematical errors, etc.). Reports, however, that contained small inconsistencies in the data (such as totals not adding up exactly) were included if the error had little effect on SNC frequencies. When reports gave sequential clutch-size data from the same colonies, I selected data from the day when the highest proportion of the clutches was complete or when the greatest number of nests was counted, providing that this day did not occur after many of the eggs had hatched.

To determine whether SNCs have increased in frequency since DDT's widespread use, all clutch-size data in the post-1950 literature and post-1950 breeding reports from the Royal Ontario Museum were compared to that in the pre-1940 literature and to the museum data using a Chi-square test corrected for continuity. If this test proved invalid for a particular species, due to a low expected frequency, the Fisher-exact probability test was used. Data collected during the 1940s were usually excluded, as DDT was just coming into use during this decade; this exclusion had little effect on the results because only a small number of studies were conducted during this period.

RESULTS

SNCs in gulls.—Evidence of supernormal clutches of five or more eggs was found in both museum egg collections and in the literature (Appendix) for seven gull species: Laughing (*Larus atricilla*), Common Black-headed (*L. ridibundus*), Mew (*L. canus*), Ring-billed, California, Herring, and Western gulls. In three additional species, the Glaucous-winged (*L. glaucescens*), Glaucous (*L. hyperboreus*), and Great Black-backed (*L. marinus*) gulls, some SNCs were found in the museum egg collections though not in the literature, owing to a lack of published reports on the clutch-size distribution for the latter two species. Furthermore, SNCs consisting of four eggs were reported in the Black-billed Gull (*L. bulleri*), Silver Gull

(*L. novaehollandiae*), and Black-legged Kittiwake (*Rissa tridactyla*), species which predominantly lay two-egg clutches. Likewise, some two-egg SNCs have been found in the Swallow-tailed Gull (*Creagrus furcata*), a species that usually lays only one egg. No SNCs were found in either the literature reports or egg collections for Lesser Black-backed (*L. fuscus*), Kelp (*L. dominicanus*), and Sabine's (*Xema sabini*) gulls.

In egg collections, SNCs were most common in Ring-billed (4.0% of all clutches), California (2.7%), and Laughing (1.9%) gulls. In the pre-1940 literature, SNCs were most frequent in Laughing (1.0%) and Ring-billed (0.5%) gulls, and in the post-1950 literature were most common in Ring-billed (1.9%), Western (1.8%), and Herring (0.3%) gulls.

SNCs in terns.—SNCs occurred in almost all tern species (Appendix). In both the museum egg collections and in the literature, SNCs of five or more eggs were found for the Gull-billed (*Sterna nilotica*), Common (*S. hirundo*), Roseate (*S. dougallii*), and Least (*S. antillarum*) terns. Furthermore, 5–6 egg clutches occurred in museum egg sets of the Forster's Tern (*S. forsteri*) although no literature reports on clutch-size distribution were found for this bird. In contrast, no SNCs were found in the egg collections of Black Terns (*Chlidonias niger*) but SNCs were reported in the nesting data collected by the Royal Ontario Museum.

In those tern species where two eggs formed the most common clutch-size—the Caspian, Arctic (*S. paradisaea*), Sandwich (*S. sandvicensis*), and Least terns—four-egg clutches (which are considered supernormal) were found in all species. Likewise, one-egg clutches predominate in the Royal (*S. maxima*), Elegant (*S. elegans*), White-fronted (*S. striata*), Black-naped (*S. sumatrana*), Sooty (*S. fuscata*) terns and the Brown Noddy (*Anous stolidus*); two-egg supernormal clutches have been reported in all of these species but the White-fronted Tern. Hence, SNCs occurred in all terns which were examined, except this last species.

In the egg collections, SNCs were most common in the Royal Tern (38.8%), Sandwich Tern (6.7%), Roseate Tern (3.7%), and Brown Noddy (3.4%). In the pre-1940 literature, SNCs were most common in the Least (7.1%), Roseate (1.9%), Royal (1.4%), Caspian (0.9%), and Sandwich (0.6%) terns. Since 1950, however, the highest frequencies of SNCs have been reported in the Sooty (12.3%), Elegant (6.7%), Caspian (2.1%), and Royal (1.7%) terns.

Change in SNC frequencies since 1950.—Based on pre-1940 and post-1950 literature reports, SNC frequencies have decreased significantly since 1950 in the Sandwich ($\chi^2 = 5.63$, $P < 0.05$), Roseate ($\chi^2 = 9.88$, $P < 0.01$), and Least ($P < 0.05$, Fisher test) terns. In contrast, SNCs have significantly increased in post-1950 literature reports in the Caspian Terns nesting in the U.S. ($\chi^2 = 5.73$, $P < 0.05$) and in Herring Gulls ($\chi^2 = 23.71$, $P < 0.01$). Surprisingly, all 43 of the reported SNCs in Herring Gulls since

1950 have been found in the Great Lakes and Ontario; 0.3% of the over 15,000 nests surveyed in this region since 1950 consisted of SNCs. Prior to 1940, no Herring Gull SNCs were found among the 72 museum egg sets collected from the Great Lakes or the 777 nests from that area reported in the literature.

Comparing the post-1950 literature with the pre-1940 egg collections revealed a higher SNC frequency in the egg collections for most gull and tern species, a result which was not surprising since many egg collectors did not collect clutches randomly. Nonetheless, in one species, the Western Gull, the SNC frequency was significantly higher in the post-1950 literature than in the egg collections ($P < 0.01$, Fisher test).

DISCUSSION

Supernormal clutches occurred in most of the gull and tern species examined, albeit in low frequencies. SNCs were found in both literature reports and egg collections for many species, thus providing independent confirmation of their occurrence.

These two sources of clutch-size data, however, pose potential problems which necessitate caution in using the results of this study to estimate SNC frequencies for many of these species. For example, in the literature reports, the paucity of clutch-size studies for most species results in a high proportion of data coming from a small area and for only a few breeding seasons. Given possible geographic and yearly variation in intraspecific clutch-size, such data may not be representative of the species as a whole. Moreover, SNC frequencies may change between the early and late part of the incubation period causing variability among studies if the eggs were counted at different times (Ryder and Somppi 1979; Conover, in press). I tried to minimize this latter problem by excluding those studies known to be conducted either early in the incubation period or when many of the eggs had already hatched. While these procedures may minimize the problem, the potential bias remains and may affect interspecific comparisons of clutch-sizes based on literature reports.

Problems with clutch-size data from museum egg collections are somewhat different. Here, hundreds of egg collectors have gathered eggs from numerous locations during the last century, minimizing the bias of single-source data. Egg collection data are probably more representative of each species as a whole, allowing for more accurate interspecific comparisons of clutch-size and SNC frequencies. However, SNCs are probably overrepresented in the egg collection data, for many collectors were not concerned with randomly sampling clutches in a colony and, instead, sought completed and unusual clutches. Consequently, SNC frequencies for any given species cannot be accurately determined from egg collections, and

comparisons between pre-1940 egg collections and the post-1950 literature can be used only to document substantial increases but not decreases in SNC frequencies since 1950.

Origin of SNCs.—Many authors have speculated on the origin of SNCs. Some have felt these clutches are the work of a single female (Glegg 1925, Marples and Marples 1934, Robinson 1934b). Most authors, however, have suggested that these large clutches occur because eggs from different females end up in the same nest, basing this hypothesis on both the large clutch-sizes and the unusual variation in egg coloration and marking patterns within some SNCs (Jones 1906, Willett 1919, Bancroft 1927, Munro 1936, Beretzk 1957, Smith 1975, Conover et al. 1979, Penland 1981).

Some authors have hypothesized that these large clutches were created when a foreign egg fell or was rolled into a nest, a phenomenon which has been demonstrated by marking eggs in only the Mew Gull (Trubridge 1980), Caspian Tern (Penland 1981), and Sooty Tern (Brown 1975). While some SNCs undoubtedly result from the above and similar occurrences—eggs falling into nests, being rolled in by the incubating birds, or from nest parasitism—in most cases these events should only increase the original clutch-size by one egg and hence not create a SNC, except in species that normally lay one-egg clutches.

Another explanation for SNCs was proposed by Hunt and Hunt (1977) when they showed that most SNCs in Western Gulls were produced by female-female pairings. Other authors have supported this conclusion, finding female-female pairs in Ring-billed Gulls (Ryder and Somppi 1979, Conover et al. 1979), California Gulls (Conover et al. 1979), Herring Gulls (Fitch 1979), Black-legged Kittiwakes (K. Chardine, pers. comm.), and Caspian Terns (Conover 1983). Some SNCs also result from polygyny in the Ring-billed Gull (Conover et al. 1979; Conover, in press), and in the Sandwich Tern (Smith 1975). Further, Nethersole-Thompson (1946) observed three adults attending a four-egg clutch in Mew Gulls; unfortunately the birds were not sexed, rendering it unclear if this was a polygynous association or a three-female group similar to the one discovered in Ring-billed Gulls by Conover (in press). Hence in most species which have been investigated, SNCs have usually resulted from multi-female associations (either polygyny or female-female pairings). The results of this study raise the possibility that female-female pairings or polygyny may occur in many gull and tern species. Furthermore, SNCs are not unique to the Laridae. Unusually large clutches have also been reported in Procellariiformes (Allen 1961, Rice and Kenyon 1962, Warham 1962, Tickell and Pinder 1966, Fisher 1968), Pelecaniformes (Snow 1960), and other Charadriiformes (Charateris 1927, Eggeling 1929, Jourdain 1936,

Bonner 1964, Drent et al. 1964, Hussell and Woodford 1965, Scott 1974, Sealy 1976, Erwin 1977). Clearly, more research is needed on the origin of SNCs in many species.

Changes in SNC frequencies since 1950.—Fry and Toone (1981) speculated that DDT may have caused an increase in female-female pairings in gulls by feminizing male embryos to the extent that these individuals do not breed as adults. If correct, the frequency of female-female pairs, and therefore SNCs, should be higher since the 1940s when DDT became widely used. For most gull and tern species, my results do not support this hypothesis. Since 1950, SNC frequencies have increased significantly in only three species: Western Gulls and Herring Gulls nesting in the Great Lakes, and Caspian Terns breeding in the United States. Of course, this recent increase in SNC frequencies in these three species may be due to causes other than DDT or female pairings. Both of these gull populations, however, nest in areas which have had problems with DDT pollution. In the Western Gull, SNCs have been reported primarily in colonies along the southern coast of California, an area which has suffered from high DDT pollution originating from the sewer systems of Los Angeles (Fry and Toone 1981). Also indicative of the high organochlorine levels in the food chain of this area is the documented problem of eggshell thinning in Brown Pelicans (*Pelecanus erythrorhynchos*) (Risebrough et al. 1971, Jehl 1973) and Double-crested Cormorants (*Phalacrocorax auritus*) (Gress et al. 1973) nesting in the area. In the Herring Gull, SNCs have only been reported in the Great Lakes but not in European colonies or in colonies located along the east coast of North America (Appendix). Herring Gulls nesting in the Great Lakes also have had a lower reproductive success than gulls nesting elsewhere, a problem which has been attributed to high levels of organochlorines in their tissues and eggs (Keith 1966, Gilbertson 1974, Gilbertson and Hale 1974, Gilbertson and Fox 1977, Gilman et al. 1977). In the Caspian Tern, SNCs have increased in frequency since 1950 in U.S. colonies but not in those located in Canada and Finland (Conover 1983). One might suspect that Caspian Terns breeding in the U.S. had higher DDT concentrations than those breeding in the more pristine parts of Canada or Finland, but there is little information on the subject. Thus, DDT or some other pollutant may have caused an increase in SNCs in Western Gulls, Herring Gulls breeding in the Great Lakes, and possibly in Caspian Terns breeding in the U.S.; for most gulls and terns, this apparently is not the case.

SUMMARY

This study examined the frequency of supernormal clutches (SNCs) in gulls and terns by checking egg collections and literature reports. Supernormal clutches were defined as clutches that contained at least 50% more eggs than the modal clutch-size, except that a two-egg

clutch was considered supernormal if 90% of the individual females lay a single egg. While SNCs were found in 15 of 18 examined gull species and 14 of 15 tern species, they constituted less than 1% of the clutches in most of these species. Most studies which have documented the causes of SNCs have shown that SNCs usually resulted from female pairings or polygynous associations. These results suggest that female pairings or polygyny may be widespread among the Laridae, as well as other normally-monogamous waterbirds. This study also tested the hypothesis that DDT has caused an increase in female pairings. If correct, there should be an increase in SNC frequencies since the late 1940s when DDT became widely used. In the Western Gull, the Great Lakes population of Herring Gulls, and the U.S. Caspian Tern population, there has been a significant increase in SNC frequencies since 1950. These two gull populations breed in areas which have had pollution problems and where high levels of organochlorines have been found in the eggs and tissues of these birds. For most gull and tern species, however, there has been no significant increase in SNC frequencies since 1950. Hence, this study's findings do not disprove this hypothesis but indicate that any pollutant-induced increase in female pairings probably is limited to a small number of species.

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Appendix

Clutch-Size Distribution in Gulls and Terns

Species	Source	No. nests	$\bar{x}$ Clutch-size	Frequency (%) 1-egg	2-egg	3-egg	4-egg	5-egg	+6-egg
Gray Gull (*Larus modestus*)									
Post-1950	Howell et al. 1972	182	1.5	46.7	51.6	1.6	0.0	0.0	0.0
Laughing Gull (*L. atricilla*)									
Pre-1940	Egg sets	425	2.9	3.5	16.5	72.2	5.9	1.4	0.5
	Mackay 1893, 1895, 1896, 1897b, 1898, 1899; Cahn 1922	392	3.0	3.8	12.2	69.6	13.3	1.0	0.0
Post-1950	Dinsmore and R. Schreiber 1974, E. Schreiber et al. 1979	932	2.6	6.7	29.0	64.0	0.2	0.0	0.0
Black-billed Gull (*L. bulleri*)									
Post-1950	Black 1955; Beer 1965, 1966	1383	1.9	26.3	62.5	10.7	0.4	0.0	0.0
Common Black-headed Gull (*L. ridibundus*)									
Pre-1940	Egg sets	647	2.9	3.7	7.6	85.8	2.6	0.2	0.2
Post-1950	Weidmann 1956; Goodbody 1955; Ytreberg 1956, 1960; Lundberg and Vaisanen 1979	1217	2.8	4.6	14.1	80.7	0.4	0.1	0.0
Mew Gull (*L. canus*)									
Pre-1940	Egg sets	403	2.7	6.4	15.1	76.7	0.7	0.7	0.2
	Belopol'skii	65	2.5	10.8	32.3	56.9	0.0	0.0	0.0
Post-1950	Ytreberg 1960, Belopol'skii et al. 1972, Campbell 1970	1327	2.8	5.0	14.5	80.3	0.1	0.1	0.0
Ring-billed Gull (*L. delawarensis*)									
Pre-1940	Egg sets	674	2.7	14.1	17.4	58.9	5.6	2.7	1.3
	Willett 1919, Moffitt 1942	575	—	← 99.5 →				0.5	0.0

APPENDIX
CONTINUED

Species	Source	No. nests	$\bar{x}$ Clutch-size	Frequency (%) 1-egg	2-egg	3-egg	4-egg	5-egg	+6-egg
Post-1950	R.O.M. reports*	38,919	2.9	1.4	10.0	87.8	0.7	0.2	0.03
	Johnston and Foster 1954, Broadbooks 1961, Vermeer 1970, Ryder 1975, Haymes and Blokpoel 1978, Blokpoel et al. 1980, Conover (in press)	6933	2.8	5.5	15.7	74.6	2.6	1.0	0.60
California Gull (*L. californicus*)									
Pre-1940	Egg sets	264	2.6	9.1	33.7	49.6	4.9	2.7	0.0
	Dawson 1923	489	2.1	13.1	59.3	27.4	0.2	0.0	0.0
Post-1950	Johnston and Foster 1954, Johnston 1956, Vermeer 1970, Conover (in press)	1943	2.7	5.7	23.2	69.5	1.5	0.1	0.0
Herring Gull (*L. argentatus*)									
Pre-1940	Egg sets	478	2.6	13.2	15.7	68.8	1.9	0.2	0.0
	Dutcher and Bailey 1903, Strong 1923, Wolfe 1923, Wood 1924, Braund and McCullagh 1940, Belopol'skii 1961, Campbell 1968	1415	2.6	1.6	36.6	61.3	0.4	0.0	0.0
	Gross 1940	10,966	1.9	34.2	38.6	27.3	0.02	0.0	0.0
Post-1950	Drost et al. 1961, Harris 1964, Keith 1966, Brown 1967, Campbell 1968, Baerends and Drent 1970, Vermeer 1971, Gilbertson and Hale 1974, Parsons 1975, Spaans and Spaans 1975, Gilman et al. 1977, Teeple 1977, Ryder and Carroll 1978, Haymes and Blokpoel 1978, Spitzer 1978	3928	2.7	6.0	18.9	74.8	0.3	0.1	0.0
	R.O.M.*	5071	2.6	12.1	21.6	63.7	2.5	0.04	0.06
	Shugart 1980	10,707	—	⟵ 99.3 ⟶			0.4	⟵ 0.3 ⟶	

APPENDIX
CONTINUED

Species	Source	No. nests	$\bar{x}$ Clutch-size	Frequency (%)					
				1-egg	2-egg	3-egg	4-egg	5-egg	+6-egg
Lesser Black-backed Gull (*L. fuscus*)									
Pre-1940	Egg sets	129	2.8	3.9	9.3	86.8	0.0	0.0	0.0
Post-1950	Harris 1964, Brown 1967	432	2.7	4.6	16.7	78.2	0.5	0.0	0.0
Silver Gull (*L. novaehollandiae*)									
Post-1950	Wheeler and Watson 1963, Mills 1973, Nicholls 1974	954	2.0	24.6	58.9	15.9	0.5	0.0	0.0
Western Gull (*L. occidentalis*)									
Pre-1940	Egg sets	855	2.9	2.6	14.0	82.3	0.9	0.1	0.0
Post-1950	R. Schreiber 1970, Harper 1971, Hunt and Hunt 1973	386	2.8	8.3	15.0	70.5	4.4	1.5	0.3
Kelp Gull (*L. dominicanus*)									
Pre-1940	Egg sets	112	2.1	33.0	25.0	41.1	0.9	0.0	0.0
Post-1950	Fordam 1964	310	2.4	9.0	42.9	48.1	0.0	0.0	0.0
Glaucous-winged Gull (*L. glaucescens*)									
Pre-1940	Egg sets	248	2.6	13.7	16.9	65.7	2.8	0.4	0.4
	Pearse 1929, Jewett et al. 1953	197	2.3	18.2	35.6	46.2	0.0	0.0	0.0
Post-1950	Drent et al. 1964, Thoresen and Galusha 1971	5106	2.6	8.5	24.4	67.0	0.1	0.0	0.0
Glaucous Gull (*L. hyperboreus*)									
Pre-1940	Egg sets	215	2.4	12.1	38.1	47.9	1.4	0.5	0.0
Great Black-backed Gull (*L. marinus*)									
Pre-1940	Egg sets	189	2.7	5.3	18.0	75.7	0.5	0.0	0.5

Appendix
Continued

Species	Source	No. nests	$\bar{x}$ Clutch-size	Frequency (%)					
				1-egg	2-egg	3-egg	4-egg	5-egg	+6-egg
Black-legged Kittiwake (*Rissa tridactyla*)									
Pre-1940	Egg sets	218	2.1	25.2	39.4	33.5	0.9	0.9	0.0
	Belopol'skii 1961	577	2.0	22.5	58.8	18.4	0.3	0.0	0.0
Post-1950	Cullen 1957; Coulsen and White 1958a, b; Coulsen 1961; Maunder and Threlfall 1972	588	2.0	13.1	76.9	10.0	0.0	0.0	0.0
Sabine's Gull (*Xema sabini*)									
Pre-1940	Egg sets	115	2.4	17.4	27.0	53.9	1.7	0.0	0.0
Swallow-tailed Gull (*Creagrus furcatus*)									
Post-1950	Harris 1970	>2000	1.0	99.9	0.1	0.0	0.0	0.0	0.0
Gull-billed Tern (*Sterna nilotica*)									
Pre-1940	Egg sets	141	2.9	2.8	23.4	61.0	12.4	0.0	0.7
	Glegg 1925	100	—	←	92.0	→	4.0	4.0	0.0
Caspian Tern (*S. caspia*)									
Pre-1940	Egg sets	282	2.2	12.8	53.5	33.0	0.7	0.0	0.0
	Conover 1983	691	—	←	99.1	→	0.9	0.0	0.0
Post-1950	U.S. colonies (Conover 1983)	5664	—	9.5	41.9	46.3	←	2.4	→
	Canadian colonies (Conover 1983)	1817	1.9	23.0	68.8	7.9	0.3	0.0	0.0
Royal Tern (*S. maxima*)									
Pre-1940	Egg sets	412	1.5	60.9	28.4	10.2	0.2	0.2	0.0
	Pemberton 1922, Bancroft 1927	73	1.0	98.6	1.4	0.0	0.0	0.0	0.0
Post-1950	Kale et al. 1965, Buckley and Buckley 1972	1245	1.0	98.3	1.7	0.0	0.0	0.0	0.0

APPENDIX
CONTINUED

Species	Source	No. nests	$\bar{x}$ Clutch-size	Frequency (%)					
				1-egg	2-egg	3-egg	4-egg	5-egg	+6-egg
Elegant Tern (*S. elegans*)									
Pre-1940	Egg sets	380	1.0	99.4	0.3	0.3	0.0	0.0	0.0
Post-1950	Gallup and Bailey 1960	30	1.1	93.3	6.7	0.0	0.0	0.0	0.0
Common Tern (*S. hirundo*)									
Pre-1940	Egg sets	548	2.7	9.8	23.5	56.0	8.9	1.1	0.5
	Mackay 1898, Witherby 1910, Rowan et al. 1918–1919, Marples and Marples 1934	3235	2.3	14.2	37.9	46.8	1.0	0.1	0.0
Post-1950	Vermeer 1967; LeCroy and Collins 1972; Lemmentyinen 1973a; Morris et al. 1976, 1980; Haymes and Blokpoel 1978	951	2.6	7.7	23.4	68.0	0.7	0.1	0.0
	R.O.M. reports*	5094	2.4	17.1	26.8	54.9	1.0	0.1	0.02
Arctic Tern (*S. paradisaea*)									
Pre-1940	Egg sets	347	2.2	11.5	55.3	30.8	2.0	0.3	0.0
	Bickerton 1912, Marples and Marples 1934, Pettingill 1939	401	1.7	38.9	54.6	6.5	0.0	0.0	0.0
Post-1950	Bengsten 1971; Joensen and Preuss 1972; Lemmetyinen 1973a, b; Coulson and Horobin 1976	1477	1.9	23.6	67.6	8.7	0.1	0.0	0.0
Forster's Tern (*S. forsteri*)									
Pre-1940	Egg sets	291	2.7	9.3	22.3	62.2	4.1	1.7	0.3

Appendix
Continued

Species	Source	No. nests	$\bar{x}$ Clutch-size	Frequency (%)					
				1-egg	2-egg	3-egg	4-egg	5-egg	+6-egg
Sandwich Tern (*S. sandvicensis*)									
Pre-1940	Egg sets	281	1.3	77.6	15.7	6.0	0.7	0.0	0.0
	Biekerton 1912; Carroll 1917; Robinson 1930, 1934a; Marples and Marples 1934	5617	1.4	57.2	42.2	0.6	0.0	0.0	0.0
	Bunyard 1909	400	—	⟵ 99.2 ⟶		0.8	0.0	0.0	0.0
Post-1950	Ansingh et al. 1960	1150	1.1	95.0	5.0	0.0	0.0	0.0	0.0
White-fronted Tern (*S. striata*)									
Post-1950	Mills and Shaw 1980	180	1.2	81.0	19.0	0.0	0.0	0.0	0.0
Black-naped Tern (*S. sumatrana*)									
Post-1950	Brant 1962	118	1.0	99.2	0.8	0.0	0.0	0.0	0.0
Roseate Tern (*S. dougallii*)									
Pre-1940	Egg sets	241	2.3	3.7	62.7	29.9	3.3	0.4	0.0
	Maekay 1895, 1896, 1897a; Marples and Marples 1934	1088	2.0	28.1	45.4	24.5	1.7	0.2	0.0
Post-1950	Robertson 1964, Britton and Brown 1971, LeCroy and Collins 1972	825	1.5	54.2	45.1	0.5	0.2	0.0	0.0
Least Tern (*S. antillarum*)									
Pre-1940	Egg sets	644	2.3	5.6	59.3	34.6	0.3	0.0	0.2
	Tout 1947 (as cited by Hardy 1957)	28	2.3	21.4	39.3	32.1	7.1	0.0	0.0
Post-1950	Swiekard 1972, Massey 1974, Napier 1978, Massey and Atwood 1981	798	2.0	14.9	66.5	18.3	0.1	0.1	0.0

Appendix
Continued

Species	Source	No. nests	$\bar{x}$ Clutch-size	Frequency (%) 1-egg	2-egg	3-egg	4-egg	5-egg	+6-egg
Sooty Tern (*S. fuscata*)									
Pre-1940	Egg sets	669	1.0	97.5	1.8	0.3	0.3	0.1	0.0
	Watson 1908	≈9429	1.0	99.7	≈0.3	0.0	0.0	0.0	0.0
1940s	Sprunt 1948	"thou-sands"	1.0	99.7–99.8	0.1–0.3	0.0	0.0	0.0	0.0
Post-1950	Brown 1975	81	1.1	87.7	12.3	0.0	0.0	0.0	0.0
Black Tern (*Chlidonias niger*)									
Pre-1940	Egg sets	633	2.8	2.8	18.3	77.1	1.7	0.0	0.0
Post-1950	R.O.M. reports*	881	2.6	9.9	20.9	67.8	1.2	0.2	0.0
Brown Noddy (*Anous stolidus*)									
Pre-1940	Egg sets	294	1.1	96.6	1.4	0.7	1.0	0.3	0.0
Post-1950	Brown 1975	11,932	1.0	98.5	1.5	0.0	0.0	0.0	0.0

* Royal Ontario Museum (Ontario Nest Records Scheme).

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DDE IN BIRDS' EGGS: COMPARISON OF TWO METHODS FOR ESTIMATING CRITICAL LEVELS

LAWRENCE J. BLUS

Since the classic study of Ratcliffe (1967) that demonstrated a decrease in eggshell weight of raptors after World War II in Great Britain, numerous studies have been conducted to determine the critical value of change in eggshell quality that will result in a serious population decline if that value is consistently equaled or exceeded over a number of years (see review by Cooke 1973). Hickey and Anderson (1968) determined that eggshell thinning of 18–26% was associated with decline or extirpation of populations of three raptorial species in the United States. The eggshell problems coincided with the widespread use of DDT after World War II, and experiments with captive Mallards (*Anas platyrhynchos*) and later with American Kestrels (*Falco sparverius*) verified that dietary DDE (a metabolite of DDT) induced eggshell thinning and reproductive impairment (Heath et al. 1969, Wiemeyer and Porter 1970, Lincer 1975).

One method for calculating the critical value of DDE in birds' eggs involves use of regression analysis; this residue value corresponds with the predetermined critical value of eggshell thinning that is associated with marked declines in other populations (Keith and Gruchy 1972, Pearce et al. 1979, Fox et al. 1980). A second method—the sample egg technique—provides a more direct measure of the critical residues of DDE and other pollutants that adversely affect nest success (Blus et al. 1974, Blus 1982, Henny et al. 1983).

The purpose of this paper is to compare and evaluate the critical values of DDE that are derived from these two methods using the Brown Pelican (*Pelecanus occidentalis*) and the Black-crowned Night-Heron (*Nycticorax nycticorax*) as the primary models.

METHODS

Brown Pelican relationships were derived from analyses of 813 eggs that were collected from 1969–1976 in California, Florida, Louisiana, and South Carolina (Blus 1982). The Black-crowned Night-Heron study involved 220 eggs that were collected from 1978–1980 in Nevada, Oregon, and Washington (Henny et al. 1983). The regression method depends on the derivation of critical values of eggshell thinning and DDE residues in eggs. A critical value of thinning is a mean calculated from a sample of eggs collected in some time interval from a population that experienced a marked decline or extirpation. Using this method, the critical residue of DDE for a particular population or species is derived from regression analysis; the critical value of thinning—≈18–20%—is then used to predict the critical residue of DDE (Keith and Gruchy 1972, Pearce et al. 1979). A test for sample size (Sokal and

Rohlf 1969:247) is recommended for determination of the number of residue analyses that are required for a statistical assessment of the mean DDE level in a sample population in relation to the critical level.

The sample egg technique was apparently used initially by Ratcliffe (1967); it involves contemporary collection of one egg from each nest in a series within a population. Nests are marked and the fate of the nest is determined. Eggs are analyzed for residues of DDE and other organochlorines, and if appropriate, for other pollutants such as certain heavy metals. Residues of each pollutant are arranged from lowest to highest, and success of each nest is then compared directly with residues in the representative egg. Effects of DDE or other residues on nest success are indicated when rate of success decreases with an increase in residues.

Determination of effects of DDE or other residues in sample eggs as related to success of individual nests is relatively straightforward; whereas extension of these results to predict effects of residues on reproductive success and status of an entire population is much more difficult. The first step is to determine a critical value of DDE or other pollutants in sample eggs; this is the lowest value that results in a marked decrease in productivity and is likely to induce a serious decline in a population in which that value is frequently equaled or exceeded. It is also useful to determine the lowest residue value that is associated with total reproductive failure.

After sampling an adequate number of eggs as outlined for the first method (Sokal and Rohlf 1969:247), the mean residue for the population is compared to the critical value. If the mean residue falls into the critical range, then the population is likely to be severely affected. Another statistical test for evaluating reduction in productivity involves calculation of the percentage of nests with sample eggs that contain critical residues. This is an important consideration because it is conceivable that the population could be affected by pollutants even though the mean residue is less than the critical value determined from individual eggs.

Contents of the eggs were analyzed individually for residues of organochlorine pesticides, their metabolites, and polychlorinated biphenyls (PCBs); analyses were completed at the Patuxent Wildlife Research Center, Laurel, Maryland. Samples were analyzed by electron-capture gas chromatography or thin-layer chromatography; residues in some samples were confirmed with use of a combined gas chromatograph/mass spectrometer. The lower limit of detection was 0.5 μg/g for the PCBs and 0.1 μg/g for the other organochlorines; residues are expressed on a fresh wet weight basis (Blus et al. 1977, Henny et al. 1983).

RESULTS

Regression analysis indicated that DDE was significantly related to eggshell thinning in Brown Pelicans ($R^2 = 0.267$, $P < 0.00001$; Fig. 1) and Black-crowned Night-Herons ($R^2 = 0.312$, $P < 0.001$), although there tended to be a wide range in eggshell thickness with a given residue level. An important factor in this relationship is the inherent variability in eggshell thickness of eggs of birds (Anderson and Hickey 1970, Klaas et al. 1974). The calculated critical threshold of DDE that is associated with 20% eggshell thinning is about 8 μg/g for the pelican and 54 μg/g for the heron. There is some evidence that the critical value for eggshell thinning may be as low as 18% in some populations (Hickey and Anderson 1968);

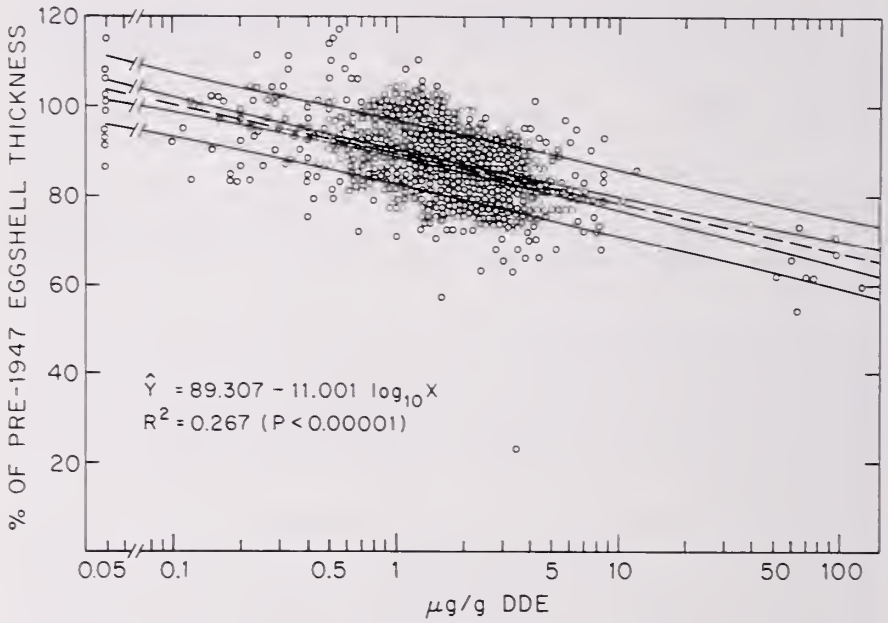

FIG. 1. Regression analysis showing the relationship of DDE residues in 813 eggs of Brown Pelicans to eggshell thickness; South Carolina, Florida, Louisiana, and California, 1969–1976. The dashed line is the regression line, the two pairs of solid lines delineate the 95% confidence limits for the population mean (inner pair) and for individual eggs (outer pair).

the critical values for DDE derived from 18% thinning are 5 μg/g for the pelican and 36 μg/g for the heron.

Using results of the sample egg technique (Fig. 2), mean nest success of Brown Pelicans arrayed by μg/g intervals of DDE ranged from 30–50% through 3 μg/g. Success was lower than expected (30%) at the ND–1 μg/g interval—probably an artifact related to the small sample size. Success was highest (50%) in the 1–2 μg/g interval and declined only slightly to 42% in the 2–3 μg/g interval. Notably, success of nests with sample eggs containing from 2.6–3.0 μg/g decreased by approximately 40% to 29% and declined precipitously above 3 μg/g; total reproductive failure occurred when DDE residues exceeded 3.7 μg/g. Thus, the critical value is 3 μg/g, that is, the lowest level of DDE that would result in severely lowered reproductive success and population decline or extirpation if it prevailed through most of the breeding population for several years.

Use of the sample egg technique for Black-crowned Night-Herons also indicated adverse effects of DDE residues on nest success. Nest success

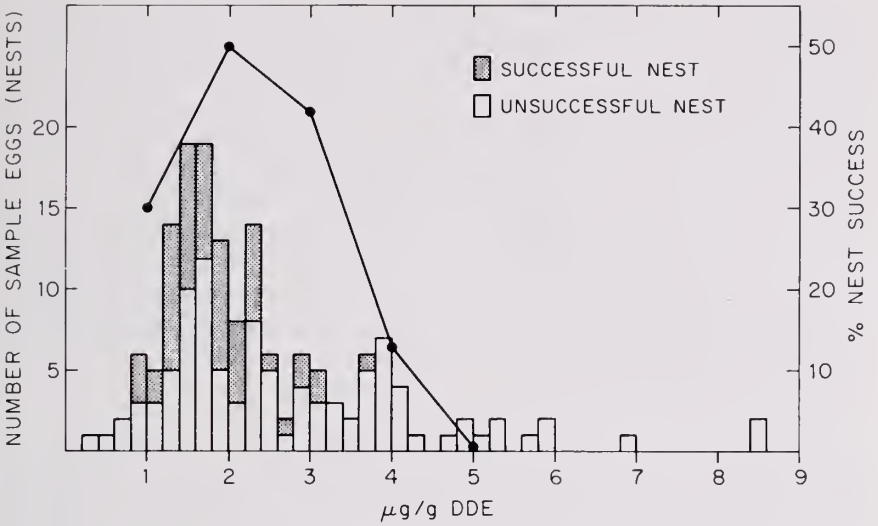

FIG. 2. Relationship of DDE residues in 156 sample eggs of Brown Pelicans to nest success. Bars represent success related to 0.2 μg/g intervals; dots on the line represent mean nest success by μg/g intervals.

ranged from 73–79% when eggs contained ≤ 8 μg/g; however, it decreased 27–58% when sample eggs contained from 8–12 μg/g. Total reproductive failure occurred only when DDE residues ranged from 25–50 μg/g. The critical level of DDE in the heron is near 12 μg/g, although the effects of DDE on nest success are extended over a wide range of residues in contrast to the precipitous decrease in success of Brown Pelican nests. The extended effects of DDE on nest success for the night heron resembled that defined for the Merlin (*F. columbarius*) in Canada (Fox 1979).

The ratio of estimated critical values of DDE that is derived from the two methods, assuming a critical thinning value of 20%, is ≃2.5:1 for the pelican and ≃4.3:1 for the heron; the respective ratios assuming a critical thinning value of 18% are ≃1.6:1 and 3.0:1. Using the critical DDE levels determined from the sample egg technique, the predicted mean eggshell thinning as derived from the regression equation is 16% at 3 μg/g (pelican) and 13% at 12 μg/g (heron).

Regarding sample size of eggs necessary to establish critical values of thinning or residues, the inherent variability (skewness) of residue data necessitates relatively large sample sizes. Regarding the Brown Pelican, the coefficient of variation (CV) calculated for DDE residues ($\log_{10}$) in a given year and locality (South Carolina) ranged from 39–61%. Using a

mean CV of 48%, power = 0.8, and $\alpha = 0.05$, 100 samples are required to be 80% certain of detecting a 20% difference between the sample mean and the critical value at the 5% level of significance. As the certainty of detection declines to 75 or 70%, the number of samples required decreases to 50 and 40, respectively. For the Brown Pelican, 40 analyses per year or over several years when residues are stable probably represents a minimal sample size that would be meaningful from a statistical standpoint. With this number, one could be assured ($P \leq 0.05$) that a residue mean that was equal to the critical value was within 30% (2.10–3.90 μg/g) of that value. From a practical standpoint, lower sample sizes may provide insight into potential problems from DDE and other organochlorines; but reliability of results decreases accordingly.

DISCUSSION

There are several possible explanations for the differences in critical values of DDE in eggs of both Brown Pelicans and Black-crowned Night-Herons, derived from the two methods. There are a number of modes of action through which DDE and other organochlorines directly affect reproductive success; these include a decline in egg production, aberrant incubation behavior, delayed ovulation, mortality of breeding adults, thinning and other deficiencies of eggshells, embryotoxicity irrespective of eggshell deficiencies, and mortality or aberrant behavior of recently hatched young (see review by Blus 1982). Thus, if only effects derived from eggshell thinning are considered, other effects are not fully accounted for and the estimated critical value of DDE is probably too high. Another possibility is that the critical value of DDE determined by the sample-egg technique is biased because of the problem of intercorrelation of residues. The organochlorine pollutants tend to be highly intercorrelated in both pelican and heron eggs, such that it is sometimes difficult to assess and quantify effects that are induced by individual pollutants. In the Brown Pelican and Black-crowned Night-Heron studies, this problem was largely ameliorated by statistical analyses and by collection of a large number of eggs from widely scattered geographic locations where there were differences in residue profiles. In deriving critical levels, errors that result from intercorrelations of residues are apparently much less serious than those that arise from the consideration of only those reproductive effects that are induced by the adverse properties of shell thinning.

A third possibility is that the critical value of shell thinning for the pelican and heron are much lower than the 18–20% derived from long-term studies showing serious decline or extirpation of populations (Hickey and Anderson 1968). Lower critical levels of shell thinning have been suggested for certain other species on the basis of short-term studies

(Capen 1977). This seems unlikely for the Brown Pelican because certain populations experience good reproductive success when shells of sampled eggs averaged 17% thinning (Blus et al. 1977).

Relying on eggshell quality as an indicator of reproductive impairment without residue analysis also has the disadvantage of eliminating effects of other pollutants such as endrin (Blus et al. 1979a) and heptachlor epoxide (Blus et al. 1979b) that act adversely on reproductive success in ways that are primarily unrelated to shell thinning. Effects of these insecticides were determined by using the sample egg technique.

Another problem that occurs in determining the critical level of DDE as interpolated from eggshell thinning data is that erroneous interpretations are likely if the regression line is arbitrarily extended beyond the data points (Snedecor and Cochran 1967) into the zone of critical thinning. For example, in studies of the Common Loon (*Gavia immer*), projections of the critical level of DDE in eggs that were related to 20% eggshell thinning ranged from 14 μg/g (Price 1977)–47 μg/g (Fox et al. 1980); residues were probably too low in both studies to adequately define the critical level of DDE. Similar interpretive problems were likely when low residues of DDE in eggs of several species of seabirds from Canada were used to predict a critical residue associated with 20% shell thinning (Pearce et al. 1979). Another example of this problem relates to the Great Blue Heron (*Ardea herodias*) in the Pacific Northwest (Blus et al. 1980). DDE residues and eggshell thinning were too low to determine critical values, but the regression line was arbitrarily extended beyond the data base for comparative purposes. This analysis indicated that a critical value of 19 μg/g of DDE was correlated with 20% eggshell thinning; whereas, the actual critical value of DDE, although not firmly established, is apparently several times higher (Vermeer and Reynolds 1970). Another example of this problem is provided by arbitrary interpolation of a regression equation that was derived from data on Brown Pelican eggs that were collected in Florida in 1969 where mean eggshell thinning was 7.5% (Blus et al. 1972b). In this regression analysis, 39 of 49 eggs contained residues ≤ 3 μg/g and the maximum residue was 6 μg/g. However, arbitrary extension of the regression line predicted a critical value of 36 μg/g that corresponded with 20% eggshell thinning. Thus, errors are likely when interpolating critical values of DDE from regression lines extending beyond the data base; these errors may result in spurious estimates that may either be much higher or lower than the true values. When sufficient eggshell thickness and residue data are available for estimating critical values of DDE from the regression equation, the estimates are meaningful but are likely to be inflated because adverse effects unrelated to eggshell thinning are not taken into account. Also, variability in thickness is too great to permit

accurate prediction of the influence of DDE on success of individual nests except when the residues are either extremely high or low (Fig. 1). For example, the 95% confidence limits for individual eggshell thickness measurements were 77% and 92% of the pre-1947 norm for sample eggs that contained 3 μg/g of DDE—compared to 95% confidence limits of 83–85% for the population mean (Fig. 1). Thus, this technique is primarily restricted to an assessment of the population effect, whereas the sample egg method may be used for predicting success of the individual nest and the population.

Establishing critical levels of pollutants in eggs and tissues of sensitive species of wildlife is a necessary procedure in assessing effects of these chemicals on individuals and populations. Once the correlative evidence from field studies is firm enough to establish a critical level, then collection of the relevant samples and proper chemical analysis is usually all that is required to demonstrate a problem situation. However, experimental interpretation of critical levels should be made when feasible in order to provide further verification of the findings in the field. The sample egg technique, although having certain disadvantages (Blus 1982) is generally more accurate in assessing critical levels of DDE than the other method. It has the advantage of simultaneous assessment of combined effects of persistent pollutants other than DDE and those induced by DDE which are unrelated to eggshell thinning. Despite these obvious differences, both methods are useful and can sometimes be used to complement one another.

SUMMARY

The sample egg technique and eggshell thickness-residue regression analysis were comparatively evaluated as tools in estimating critical levels of DDE in birds' eggs that seriously affect reproductive success and population starts.

In comparing critical values of DDE that were derived from the two methods, the estimates were lower using the sample egg technique for both the Brown Pelican (3 μg/g vs 8 μg/g) and the Black-crowned Night-Heron (12 μg/g vs 54 μg/g) assuming a critical value of eggshell thinning at 20%.

Extension of the regression line beyond the eggshell thickness-DDE residue data base is likely to result in spurious critical values of DDE. When sufficient thickness and residue data are available for estimating critical values of DDE from the regression equation, the estimates are meaningful but are likely to be inflated because adverse effects unrelated to eggshell thinning such as parental behavior and embryotoxicity unrelated to eggshell deficiencies are not taken into account.

Establishing critical levels of pollutants in eggs and tissues is a necessary procedure in assessing effects of these chemicals on individuals and populations of sensitive species. There are inherent difficulties in quantifying the effects of any pollutant on population trends and declines in productivity. The sample egg technique is apparently a more sensitive method for estimating critical levels of DDE, but some subjective interpretation is required for results obtained by both methods.

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U.S. FISH AND WILDLIFE SERVICE, PATUXENT WILDLIFE RESEARCH CENTER, PACIFIC NORTHWEST FIELD STATION, 480 SW AIRPORT RD., CORVALLIS, OREGON 97333. ACCEPTED 7 JULY 1983.

WILSON ORNITHOLOGICAL SOCIETY STUDENT MEMBERSHIP AWARDS

Student membership awards in the Wilson Ornithological Society are available for persons who are not currently members of the society. The competitive awards are made available from the general funds of the society to recognize students who have the potential to make significant contributions to ornithology. Application forms for the awards to be granted in 1985 may be obtained from Richard N. Conner, Southern Forest Experiment Station, P.O. Box 7600 SFA, Nacogdoches, TX 75962. **The deadline for applying is 1 November 1984.** A Wilson Ornithological Society Student Membership Award provides a 1 year membership in the Wilson Ornithological Society for successful nominees.

GENERAL NOTES

Wilson Bull., 96(2), 1984, pp. 277–286

A morphometric comparison of Western and Semipalmated sandpipers.—Semipalmated (*Calidris pusilla*) and Western (*C. mauri*) sandpipers are common migrant shorebirds of the east and west coasts of North America, respectively. Identification of these species can be notoriously difficult. In the field this can be accomplished by behavioral differences that include call notes (Bent, U.S. Natl. Mus. Bull. 142, 1927; Wallace, Br. Birds 67:1–17, 1974), feeding microhabitat (Recher, Ecology 47:393–407, 1966; Ashmole, Auk 87:131–135, 1970), and flight posture (Palmer, pp. 143–267 *in* The Shorebirds of North America, E. Stout, ed., Viking, New York, New York, 1967). In spring plumage, these species are more readily separable, *C. mauri* shows extensive chestnut on the crown and on the dorsum, and greater amounts of spotting on the breast and flanks than does *C. pusilla* (Palmer 1967). In winter plumage, however, the two species are difficult to distinguish. Size differences are known; *C. mauri* generally has a longer bill (Ouellet et al., Can. Field-Nat. 87:291–300, 1973; Fig. 1, this study). Frequently birds in winter plumage are hard to separate by bill length alone.

Ouellet et al. (1973) found considerable overlap in bill size. They used sexed museum study-skins and graphically contrasted two bill measurements which yielded a maximum separation between the species. Because of the broad overlap *C. pusilla* and *C. mauri* seemed morphometrically inseparable.

I analyzed mensural data from museum study skins and skeletons of *C. pusilla* and *C. mauri* to determine if these species are indeed morphometrically distinct. My primary objectives were: (1) to quantify and compare the phenetic differences between the two species and their sexes; and (2) to provide species- and sex-differentiating criteria for problematic skeletal and study-skin specimens.

Methods.—I measured study skins and skeletons of *C. mauri* and *C. pusilla* taken during breeding or on migration. No juvenile birds taken from July through December were measured, because many likely do not reach full adult dimensions in this interval. I measured 22 characters on skeletons to the nearest 0.1 mm, using dial calipers (Fig. 2). I measured 49 male and 61 female *C. pusilla,* taken in autumn during migration (N = 90) from southern Canada and the northern United States and from the Arctic breeding grounds (N = 20), and 42 male and 41 female *C. mauri,* taken in autumn migration (N = 65), and from the breeding grounds (N = 18).

I measured the following variables on study skins (estimated measurement error in parentheses): exposed culmen (0.2 mm), distance from distal portion of nostril to tip of bill (0.2 mm), tarsus length (0.5 mm), and natural (unflattened) wing length (1.0 mm). Characters measured but discarded due to low measurement repeatability were: bill width (across the base of the nostrils), tail length, and phalanx length. In the study skin analyses, I measured 147 male and 107 female *C. pusilla,* and 51 male and 52 female *C. mauri,* all taken with a similar seasonal and geographic distribution as the skeletal material.

For the skeletal data set, missing values were estimated with the BMDP-AM procedure (Dixon and Brown, Biomedical Computer Programs, P-series, Univ. Calif. Press, Berkeley, California, 1979). Specimens missing more than three measurements were not used.

I used direct and stepwise discriminant functions analysis (DFA; Nie et al., Statistical Package for the Social Sciences, McGraw-Hill, New York, New York, 1975). In all analyses, except where noted, the "direct" method was used to analyze those variables with means differing between groups (species or sexes) by at least 0.1 mm (measurement error). Hence, I minimized the consideration of univariate differences attributable solely to measurement error.

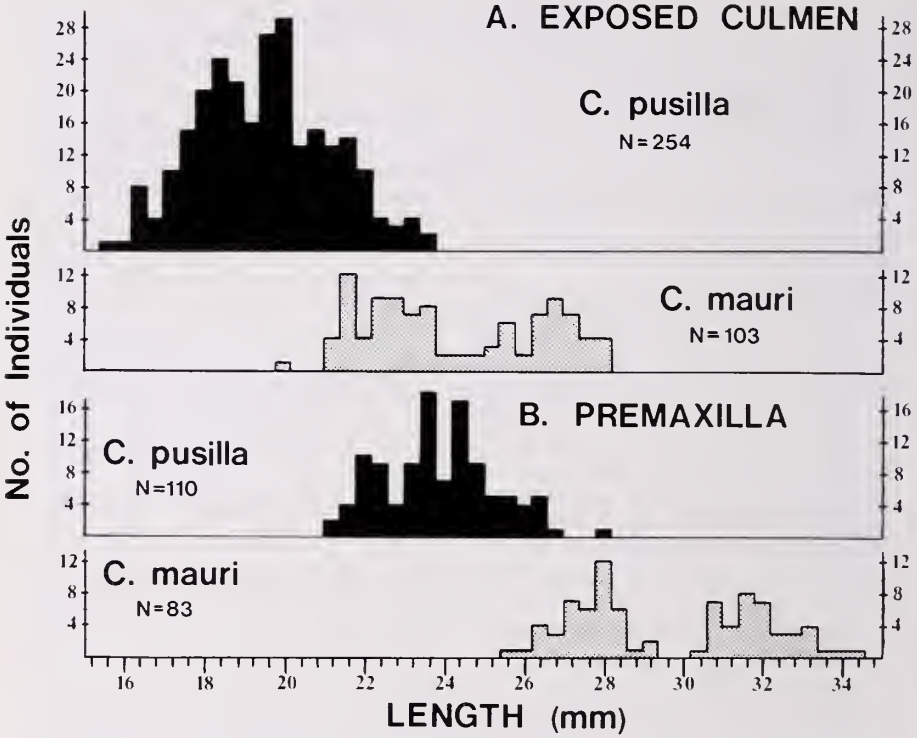

FIG. 1. Bill measurements from study skins (exposed culmen) and skeletons (premaxilla) showing the degree of overlap between the two species on this character which best discriminates between the two species. (Species identification of birds in [B] verified correct from Fig. 3.)

To establish species-discriminating criteria, I used a "known" (correctly identified) sample of birds from each species, irrespective of sex and chosen by their collecting locality and season. I assumed that a bird could correctly be identified as *C. mauri* when collected in breeding plumage (April to July, Palmer 1967), or on the west coast of the United States. Similarly, a "known" *C. pusilla* was one collected in breeding plumage (April to July, Palmer 1967), and/or in arctic or eastern Canada. To separate the species, a DFA using "knowns" only was performed. This allowed the "unknowns" to be verified. Classification of all "unknowns" (birds not conforming to the above criteria) corresponded to identity on spec-

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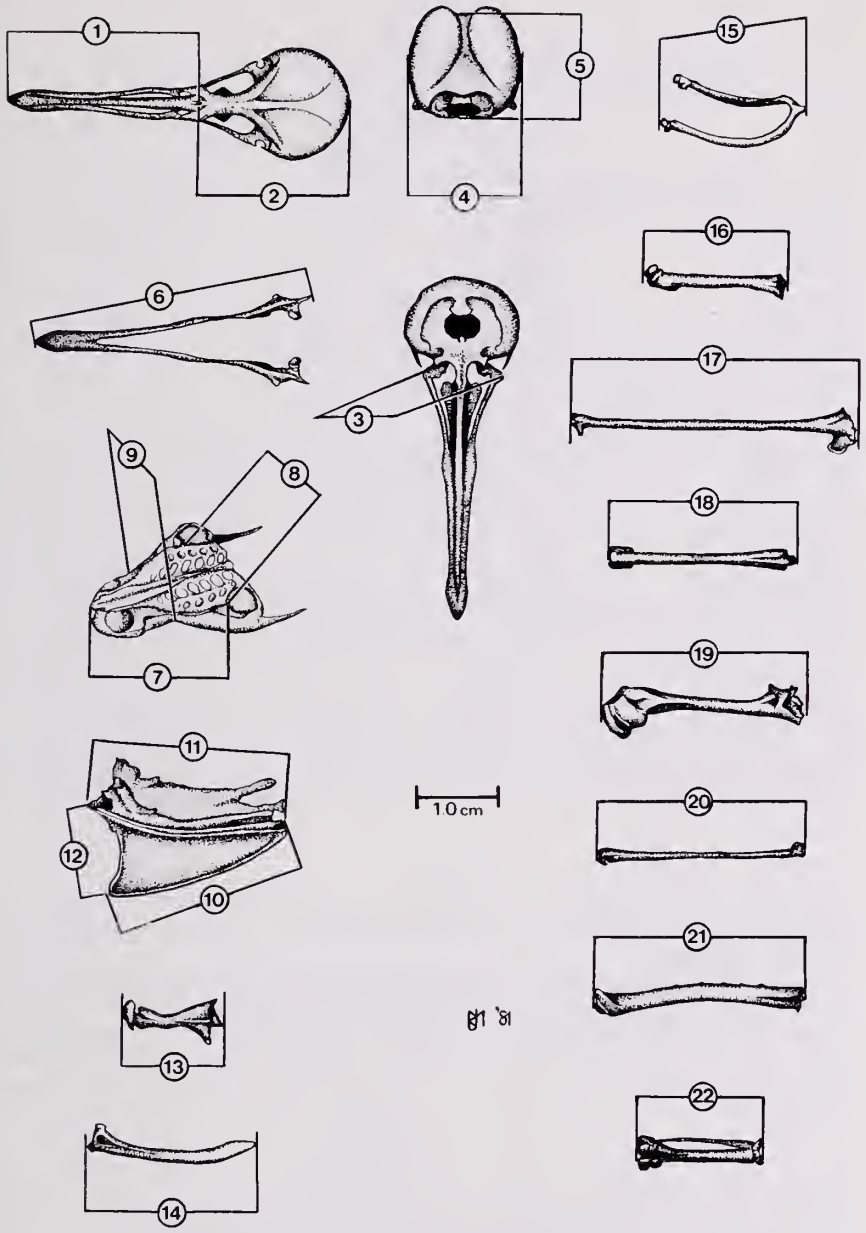
FIG. 2. Skeletal elements from *C. pusilla*, showing the 22 measurements used in this study: (1) premaxilla length (to base of depression in skull); (2) skull length; (3) quadrate length; (4) skull width; (5) skull depth; (6) mandible length; (7) anterior synsacrum length; (8) posterior synsacrum width; (9) anterior synsacrum width (across narrowest portion); (10)



keel length; (11) sternum length; (12) keel depth; (13) coracoid length; (14) scapula length; (15) furcula length; (16) femur length; (17) tibiotarsus length; (18) tarsometatarsus length; (19) humerus length; (20) radius length; (21) ulna length; (22) carpometacarpus length.

TABLE 1

SKELETAL MEASUREMENT STATISTICS FOR *C. PUSILLA* AND *C. MAURI*

Character	*C. pusilla*		*C. mauri*	
	Males (N=49) $\bar{x} \pm SD$	Females (N=61) $\bar{x} \pm SD$	Males (N=42) $\bar{x} \pm SD$	Females (N=41) $\bar{x} \pm SD$
Premaxilla length	23.2 ± 1.13	24.3 ± 1.37	28.0 ± 1.56	31.4 ± 1.64
Skull length	16.4 ± 0.36	16.4 ± 0.34	16.7 ± 0.23	16.7 ± 0.21
Quadrate length	9.8 ± 0.23	9.9 ± 0.24	10.3 ± 0.27	10.4 ± 0.22
Skull width	12.3 ± 0.20	12.3 ± 0.20	12.7 ± 0.20	12.7 ± 0.21
Skull depth	10.8 ± 0.19	10.8 ± 0.20	11.1 ± 0.14	11.1 ± 0.18
Mandible length	30.3 ± 1.15	31.6 ± 1.31	34.6 ± 1.55	37.6 ± 1.74
Anterior synsacrum length	12.2 ± 0.33	12.6 ± 0.44	12.2 ± 0.41	12.7 ± 0.38
Posterior synsacrum width	12.6 ± 0.36	12.7 ± 0.41	12.9 ± 0.34	13.3 ± 0.36
Anterior synsacrum width	8.3 ± 0.31	8.5 ± 0.41	8.6 ± 0.29	9.0 ± 0.30
Keel length	24.3 ± 0.65	24.4 ± 0.71	23.5 ± 0.71	24.2 ± 0.65
Sternum length	25.4 ± 0.65	25.8 ± 0.74	25.3 ± 0.64	26.1 ± 0.57
Keel depth	12.7 ± 0.32	12.9 ± 0.49	13.4 ± 0.39	13.7 ± 0.37
Coracoid length	12.1 ± 0.25	12.3 ± 0.35	12.1 ± 0.35	12.5 ± 0.24
Scapula length	19.9 ± 0.55	20.3 ± 0.72	19.8 ± 0.53	20.4 ± 0.53
Furcula length	15.5 ± 0.48	15.9 ± 0.51	16.2 ± 0.47	16.5 ± 0.51
Femur length	16.9 ± 0.40	17.4 ± 0.58	17.1 ± 0.41	17.6 ± 0.51
Tibiotarsus length	35.4 ± 1.03	36.2 ± 1.16	36.3 ± 1.00	37.9 ± 1.07
Tarsometatarsus length	21.8 ± 0.74	22.2 ± 0.84	22.5 ± 0.71	23.7 ± 0.75
Humerus length	24.0 ± 0.55	24.6 ± 0.76	24.2 ± 0.61	25.0 ± 0.55
Radius length	24.3 ± 0.61	24.9 ± 0.75	24.2 ± 0.62	25.1 ± 0.61
Ulna length	25.3 ± 0.73	26.0 ± 0.77	25.3 ± 0.59	26.1 ± 0.64
Carpometacarpus length	14.8 ± 0.39	15.2 ± 0.50	15.0 ± 0.37	15.5 ± 0.41

imen labels, consequently data for "knowns" and "unknowns" were pooled and tested again. A DFA was performed between sexes for each species separately to contrast sexual differences between the species.

Results.—All DFA's presented were highly significant ($P < 0.001$). Box's M was used to test for equality of expected covariance matrices (Nie et al. 1975). Only that DFA discriminating *C. mauri* sexes had non-equal covariance matrices ($P = 0.28$). This latter analysis, however, was performed on large nearly equal sample sizes, therefore the DFA is likely sufficiently robust to allow a departure from this assumption (see Ito and Schull, Biometrica 51:71–82, 1964).

(1) Skeletal analyses.—The DFA for species separation based on 16 variables (Table 1) shows a complete separation of the species (Table 2, col. 1; Fig. 3). There were, however, two apparently misidentified "knowns" (Fig. 3): a female identified as a *C. mauri* collected on 23 March 1953 in Washington (Univ. Washington, WSM 14177), which falls into the range of *C. pusilla,* but probably is a Least Sandpiper (*C. minutilla*) (S. Rohwer, pers. comm.); and a male identified as a *C. pusilla* collected on 21 April 1976 in Kansas (KU 70344), which probably is a *C. mauri.* These questionable specimens were subsequently excluded from all DFAs.

TABLE 2

STANDARDIZED AND UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS FOR SKELETAL ANALYSES[a]

Character	Standardized DF coefficients				Unstandardized DF coefficients			
	Species	Species (min. no.)	*C. pusilla* sexes	*C. mauri* sexes	Species	Species (min. no.)	*C. pusilla* sexes	*C. mauri* sexes
Premaxilla length	0.771	0.942	−0.085	−1.28	0.4544	0.5079	−0.0672	−0.8021
Skull length	0.004	—	—	—	0.0140	—	—	—
Quadrate width	0.179	—	—	—	0.7143	—	—	—
Skull width	0.384	0.502	—	—	1.9248	2.5134	—	—
Skull depth	0.213	—	—	—	1.2020	—	—	—
Mandible length	0.210	—	0.707	0.489	0.1173	—	0.5693	0.2978
Anterior synsacrum length	—	—	—	0.101	—	—	—	0.2571
Posterior synsacrum width	−0.158	—	—	0.245	−0.4015	—	—	0.6970
Anterior synsacrum width	0.065	—	—	−0.305	0.1783	—	—	−1.0318
Keel length	−0.447	−0.439	—	−0.257	−0.6131	−0.6020	—	−0.3757
Sternum length	—	—	−0.212	−0.224	—	—	−0.3005	−0.3683
Keel depth	0.422	0.390	—	—	1.0397	0.9599	—	—
Coracoid length	—	—	—	−0.134	—	—	—	−0.4507
Scapula length	—	—	—	0.281	—	—	—	0.5299
Furcula length	−1.68	—	0.269	−0.0496	−0.0496	—	1.1660	0.5563
Femur length	−0.027	—	0.590	0.258	−0.0496	—	0.5449	0.559
Tibiotarsus length	−0.317	—	−0.063	−0.350	−0.2509	—	−0.0572	−0.3383
Tarsometatarsus length	0.243	—	−0.199	−0.209	0.2723	—	−0.2512	−0.2866
Humerus length	−0.382	−0.544	−0.131	−0.057	−0.5391	−0.7677	−0.1934	−0.0983
Radius length	—	—	−0.084	1.097	—	—	−0.1257	1.7986
Ulna length	—	—	−0.051	−0.461	—	—	−0.0688	−0.7503
Carpometacarpus length	−0.043	—	0.433	−0.290	−0.0882	—	0.9849	−0.7447
Wilk's Lambda	0.1306	0.1448	0.3722	0.7042	—	—	—	—
Constant	—	—	—	—	−31.0569	−24.0063	−34.5717	21.4317

[a] $P < 0.001$ in all cases.

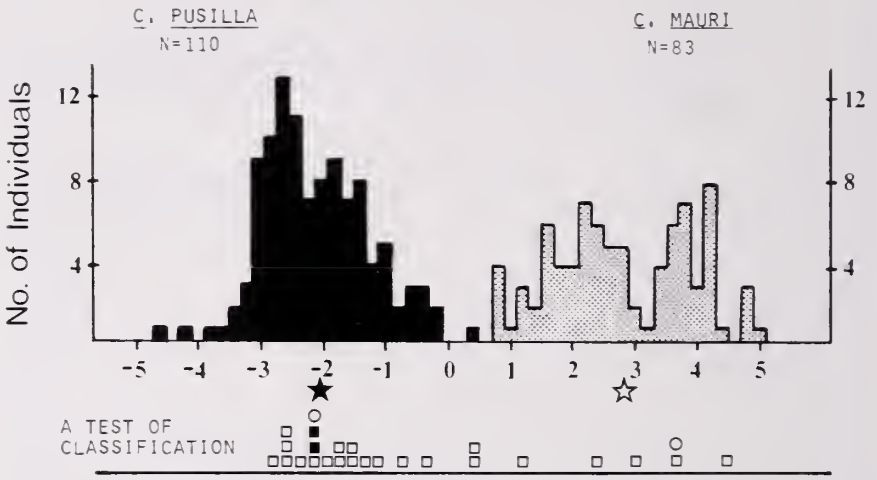


FIG. 3. Species discrimination based on five skeletal characters. The discriminant function axis is in standard deviation units. The mean (★) of *C. pusilla* is −2.1 and that of *C. mauri* (☆) is 2.8. The 95% confidence limits for individual values spans two discriminant function units either side of the mean. A test of the accuracy of the classification function is provided (○ = mis-classified "known," ■ = mis-classified "unknown," and □ = correctly classified "known").

As shown by standardized discriminant function coefficients (SDFCs), species were separated most by skull measurements, especially premaxilla length (Table 2, col. 1).

A stepwise DFA showed total separation between species can be achieved with only five characters. Relatively long wings and long keel in *C. pusilla* are contrasted with a large skull and deep keel in *C. mauri* (Table 2, col. 2). These results were tested by classifying 22 "knowns" previously excluded because each had at least four missing values, but all had values for the five species-separating variables. All 22 were correctly classified based on label identity (Fig. 3).

Sexes of *C. pusilla* overlap broadly in morphometric characters (Fig. 4, overlap = 84.5%). DFA correctly classified the sex in only 74.8% of the individuals (81% of females, 66.7% of males). Lengths of mandible, femur, and carpometacarpus were the most important discriminating characters (Table 2, col. 3). Sexual dimorphism in *C. mauri* (Fig. 5, overlap = 65.8%) is stronger than in *C. pusilla*, with premaxilla and radius lengths most important in discriminating between males and females (Table 2, col. 4). DFA correctly classified to sex 88.6% of the individuals (87.2% of females, 90% of males).

Skeletal material can easily be identified by using unstandardized discriminant function coefficients (UDFCs, see Table 2). Determination of species or sex of an unknown specimen requires summing of the products of all raw measurements with their UDFCs, and adding of the constant. The resultant value (the discriminant score) can then be used to assign the specimen in question to the most likely group, through comparison with the appropriate figure (Figs. 3, 4, 5).

(2) Study-skin analyses.—Combination of study-skin variables (in a DFA) was better than univariate measures in differentiating between sexes only for *C. pusilla*. Improvements in discrimination for bill length alone were: 1.4% for species separation, 1.0% for *C. mauri*

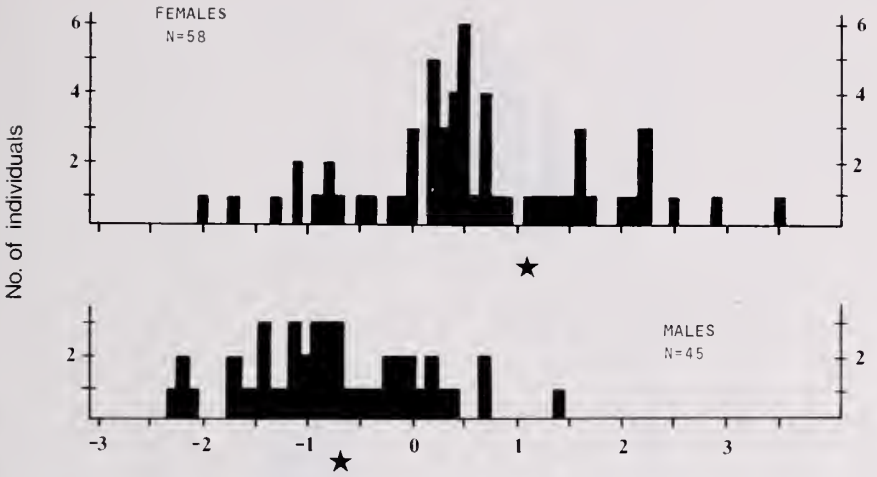


FIG. 4. Discriminant function for sexes of *C. pusilla,* based on 11 skeletal variables. The mean (★) for males is −0.7 and that for females is 1.1. The 95% confidence limits for individual values spans two discriminant function units on either side of the mean.

sexual separation, and 9.8% for *C. pusilla* sexual discrimination. Hence only univariate information is provided for the former two, while SDFCs and UDFCs are provided for *C. pusilla* sexual discrimination (Table 3). This DFA correctly separated 83.1% of the 254 individuals (78% of females, 87% of males). In comparison, Harrington and Taylor (J. Field Orn. 53:174–177, 1982) were only able to sex 40% of their 45 *C. pusilla,* by contrasting wing and bill lengths and constructing 95% confidence ellipses.

Bill lengths of *C. mauri* fall into two discrete groups (Fig. 2), corroborating the studies of Page and Fearis (Bird-Banding 42:297–298, 1972) and Phillips (Am. Birds 299:799–806, 1975), in which 91% and 98%, respectively, of individuals were correctly sexed by bill length. Each group actually contains an assortment of both sexes, raising the possibility that if these groups are subdivided according to sex, some mis-sexed specimens must have been included. I have accepted all sex identifications because there is no way now of ascertaining their correctness. The extreme outliers in Figs. 4 and 5, however, may be attributable to mis-sexed specimens.

Inter-sexual differences are considerably greater in *C. mauri* (Fig. 5) than in *C. pusilla* (Figs. 1, 4). Geographic variation might explain the relative lack of dimorphism found for *C. pusilla* in this study. Palmer (1967) speculates on the existence of three possibly disjunct populations: eastern, central, and western. Harrington and Morrison (Stud. Avian Biol. 2: 83–100, 1979) document a cline of decreasing bill and wing size from east to west. I compared degree of sexual dimorphism in three groups of *C. pusilla* taken on the breeding grounds with the dimorphism in the total sample. The three samples represented western (northern Yukon Terr. to western Victoria Island and south to Fort Thompson, N.W.T.; 14 females, 27 males), central (eastern Victoria Island to Melville Peninsula and south to the NW shore of Hudson Bay; 8 females, 26 males), and eastern (Baffin Island through Ungava to the Belcher Islands; 13 females, 27 males) breeding populations (Palmer 1967), and as such they do not necessarily represent discrete populations. When the four study-skin variables were standardized (to remove the effect of absolute size), the Euclidean distances between

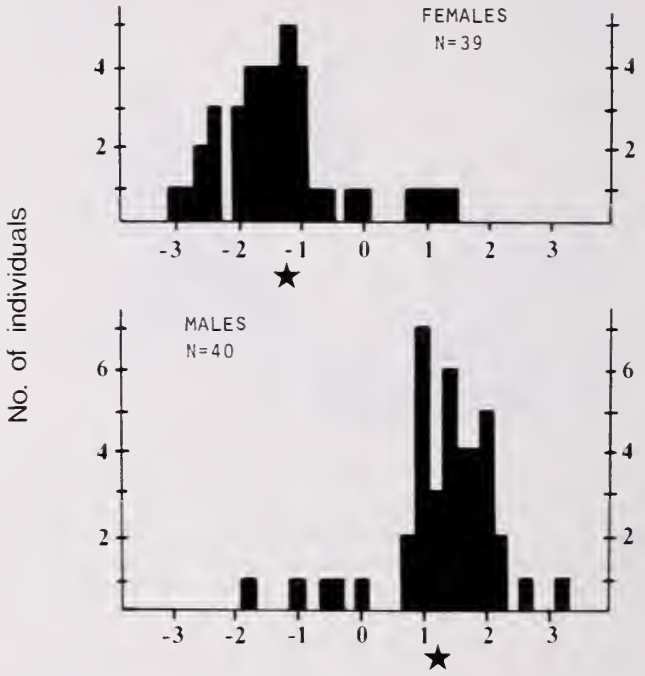


FIG. 5. Discriminant function for sexes of *C. mauri*, based on 16 skeletal characters. The mean (★) for males is 1.3 and that for females is −1.3. The 95% confidence limits for individual values spans two discriminant function units on either side of the mean.

means for males and females in each geographic group were calculated as: *C. pusilla*—western, 2.575; central, 2.100; eastern, 2.553; *C. mauri*—3.039. Even when treated as above, *C. pusilla* is less dimorphic than *C. mauri*.

Discussion.—I have here reaffirmed the phenetic distinctiveness of *C. pusilla* and *C. mauri*. However, because analyses of study-skin measurement characters produced no strong separation between species, perhaps these species cannot be completely separated by measurements alone. Results from my geographic variation and sexual dimorphism assays suggest two questions for future study: (1) Why is *C. mauri* more sexually dimorphic than *C. pusilla*? (2) Why are the two species most dissimilar in sympatry, and most similar where they are farthest apart?

One hypothesis to account for the differing degrees of sexual dimorphism in these species is that latitudinally different wintering regions for *C. mauri* sexes (Page et al., Calif. Birds 299:799–806, 1972) selectively favor different bill lengths. Recent work on the importance of mortality on the wintering grounds (e.g., Page and Whitacre, Condor 77:73–83, 1975) supports this speculation.

That *C. pusilla* and *C. mauri* are most dissimilar in sympatry and most similar in allopatry suggests character displacement. Indeed, recent behavioral work (Connors, A.O.U. annual meeting scientific paper abstract, 1983) has found that sympatric territorial males of *C. pusilla* and *C. mauri* spent almost as much time chasing males of the other species as they did chasing conspecifics.

TABLE 3
MEASUREMENT STATISTICS FOR STUDY SKINS

Variable	*C. pusilla*						*C. mauri*			
	Males		Females				Males		Females	
	($N = 147$) $\bar{x} \pm SD$	Range	($N = 107$) $\bar{x} \pm SD$	Range	SDFC[a,b]	UDFC	($N = 51$) $\bar{x} \pm SD$	Range	($N = 52$) $\bar{x} \pm SD$	Range
Exposed culmen	18.6 ± 1.36	15.5–23.0	20.5 ± 1.38	17.5–23.7	−0.623	−0.4555	22.6 ± 1.08	20.5–26.5	25.9 ± 1.84	21.0–29.0
Nostril to bill tip	15.2 ± 1.17	12.8–18.1	16.9 ± 1.28	13.2–19.9	0.073	0.0602	18.8 ± 0.97	17.2–22.9	22.0 ± 1.68	17.1–24.6
Tarsus length	21.2 ± 0.74	19.4–23.4	22.1 ± 0.63	20.0–23.9	−0.535	−0.7674	21.7 ± 0.71	19.8–22.7	23.2 ± 0.88	21.4–25.1
Wing length	93.6 ± 2.10	87.5–98.5	96.1 ± 2.40	90.0–101.0	−0.326	−0.1470	93.0 ± 1.80	89.5–97.0	96.1 ± 2.80	90.0–101.0
Constant						38.3385				

[a] Wilk's Lambda = 0.5584 ($P < 0.001$).
[b] 95% confidence limits for SDFCs: males: −1.2–2.8 ($\bar{x} = 0.8$); females: −3.0–1.0 ($\bar{x} = -1.0$).

The measurements provided here are of use to workers attempting to identify species and sex of problematic museum specimens for these two sandpipers. This species-separating information must be applied with caution, since the possibility of confusion with other sandpiper species, especially Palearctic ones, exists. For North America, though, only the skull of *C. minutilla* is likely to be similar in size to *C. pusilla*, and this species has a distinctive bill shape (Prater et al., Guide to the Identification and Ageing of Holarctic Waders, Maud and Irvine, Tring, Herts., England, 1977).

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Macrohabitat use, microhabitat use, and foraging behavior of the Hermit Thrush and Veery in a northern Wisconsin forest.—*Catharus* is one of several genera of North American passerines (e.g., *Dendroica, Empidonax, Parus, Toxostoma, Vireo*) that has received particular attention from ecologists (Grinnell, Auk 34:427–433, 1917; MacArthur, Ecology 39: 599–619, 1958; Lack, Am. Nat. 103:43–49, 1969; Beaver and Baldwin, Condor 77:1–13, 1975; James, Wilson Bull. 88:62–75, 1976). These researchers addressed the question of how series of congenerics differ ecologically to promote sympatric coexistence. Dilger (Auk 73:313–353, 1956a; Wilson Bull. 68:170–199, 1956b; Syst. Zool. 5:174–182, 1956c) arranged the four *Catharus* thrushes and the related *Hylocichla mustelina* along a synthetic gradient based on morphology, behavior, macrohabitat use, and geographical and elevational distributions. Of these factors, subsequent studies of interspecific interactions focused on macrohabitat use (Morse, Wilson Bull. 83:57–65, 1971; 84:206–208, 1972; Sealy, Condor 76:350–351, 1974; Bertin, Condor 79:303–311, 1977; Noon, Ecol. Monogr. 51:105–124, 1981). Relatively little information exists on the behavioral mechanisms behind the observed patterns.

To examine the relationship of *Catharus* thrushes to their habitat, I chose two sympatric species occupying adjacent, intermediate positions on Dilger's morphological-ecological gradient, the Hermit Thrush (*C. guttatus*) and the Veery (*C. fuscescens*). Data were collected for interspecific comparisons of habitat relationships at three levels of detail: (1) the structure of the two species' habitats (macrohabitat use); (2) species' use patterns for vegetation types and height strata within these habitats (microhabitat use); and (3) movement rates and lengths and prey capture methods (foraging behavior).

Based on the observations of earlier workers (Bent, U.S. Natl. Mus. Bull. 196, 1949; Dilger, 1956b, c; Morse 1971; Eckhardt, Ecol. Monogr. 49:129–149, 1979; Noon 1981), I made the following predictions. (1) Hermit Thrushes would occupy available sites dominated by coniferous vegetation, while Veeries would occupy sites dominated by deciduous vegetation. (2) Hermit Thrushes would be active primarily on the ground, whereas Veeries would

TABLE 1
TREE SPECIES AND SHRUB GENERA IN HERMIT THRUSH AND VEERY TERRITORIES

Vegetation category[a]	Species or genera[b]
Hardwoods	*Betula papyrifera*
	Acer saccharum
	Quercus borealis
	Acer rubrum
	Prunus spp.
Aspens	*Populus tremuloides*
	Populus grandidentata
Conifers	*Pinus resinosa*
	Picea mariana
	Pinus strobus
	Abies balsamea
	Picea glauca
	Tsuga canadensis
Shrubs	*Corylus*
	Alnus
	Viburnum
	Cornus
	Rubus
	Vaccinium
	Lonicera
	Amelanchier
	Campostoma
	Salix
	Myrica

[a] Categories based on growth form and foliage structure.
[b] Taxa are ranked in order of decreasing abundance within each category.

engage in more arboreal activities. Within the trees, Veeries would concentrate their activities in deciduous species and Hermit Thrushes would selectively use conifers. (3) Hermit Thrushes would rely more frequently on the active search patterns associated with ground foraging, whereas Veeries would employ more arboreal and aerial prey captures and sit-and-wait foraging tactics.

Study area and methods.—The study area was centered at the University of Wisconsin Trout Lake Station and the adjacent Mann Creek Wildlife Area, Vilas Co., Wisconsin (46°01′N, 89°40′W). The region is primarily forested with a mixture of conifers, aspens, and northern hardwoods (Table 1). Both thrushes were common and their territories frequently adjoined or overlapped.

I recorded vegetational data for three representative territories of each species. A territory was defined as an area regularly occupied by a singing male thrush. For each territory, these data consisted of the following measures: (1) tree identity and size (Tables 1, 2), (2) overstory structure (Table 2), and (3) understory composition and structure (Tables 1, 2).

For habitat analysis I classified woody species in four vegetation types based on overall

TABLE 2

VEGETATION STRUCTURE OF HERMIT THRUSH AND VEERY TERRITORIES[a]

	Percent occurrence of tree types and size classes					
	Tree types[b]			Tree size classes[b]		
	% hardwoods	% aspens	% conifers	% saplings (BA < 100 cm²)	% intermediate (100 cm² ≤ BA < 300 cm²)	% mature (BA ≥ 300 cm²)
Hermit Thrush (N = 134)	24%	57%	19%	69%	12%	19%
Veery (N = 126)	21%	59%	20%	56%	17%	27%

	Structure of canopy and understory							
	Canopy structure[c]				Understory structure[d]			
	Foliage 3 m–9 m only	Foliage >9 m only	Foliage 3 m–9 m and >9 m	No foliage	Low herb growth (<0.25 m)	Tall herb growth (0.25–1.0 m)	Low woody growth (<1.5 m)	Tall woody growth (1.5–3.0 m)
Hermit Thrush	15%	25%	42%	18%	19%	19%	34%	28%
Veery	12%	20%	51%	17%	15%	18%	37%	30%

[a] Based on three territories for each species.
[b] Based on stem counts of trees >1 m in height in six randomly located 0.01-ha circular quadrats (two per territory).
[c] Canopy structure is presented as the percentage of 60 randomly located vertical sightings (20 per territory) which intersected vegetation at 3 m–9 m, >9 m, both heights, or neither.
[d] Understory structure is presented as the percentage of 600, 1-m transect segments (200 per territory, collected along two 100-m transects) which contained vegetation in four growth categories.

growth form and foliage structure (Table 1): (1) shrubs, (2) hardwoods, (3) aspens, and (4) conifers. I also delineated five height strata: 0 m, 0–3 m, 3–6 m, 6–9 m, and >9 m—hereafter referred to as ground, 3 m, 6 m, 9 m, and >9 m.

I collected behavioral data on eight pairs of Hermit Thrushes and seven pairs of Veeries between 1 June and 15 August 1976. I observed these territorial birds on a regular basis and followed them for several hours during each observation period. Data from all sequences and individuals were eventually pooled, since a qualitative inspection of the results revealed no appreciable intergroup variability. Observation time totalled 430 min for the Hermit Thrush and 432 min for the Veery.

Behavioral data consisted of chronological records written in a notebook and timed with a stopwatch calibrated in 0.01-min intervals. Individual birds were visually located and chronicled until I lost sight of them. Typically, continuous timings lasted only a few min ($\bar{x}$ = 1.8 min, SD = ±2.9, N = 449). For each movement, the following information was recorded: (1) starting perch location, including ground, tree or shrub species, size category for trees, and height; (2) movement length and type: nonfeeding which included simple travel, aggressive interactions, nest visits, etc.; or feeding which included attempted or realized prey captures; and (3) subsequent perch location (same data as starting location). I visually estimated heights and distances.

In analyzing microhabitat use, I included both feeding and nonfeeding activities. An animal's ability to move through an environment, defend a portion of it, or care for its young can be as important in determining the suitability of a particular habitat as the animal's success at procuring food (Pleszczynska, Science 201:935–937, 1978; Gatz, Tulane Studies Zool. Bot. 21:91–124, 1979; Moermond, Behaviour 70:147–167, 1979).

When a bird did attempt to capture prey, I recorded feeding method, location, and

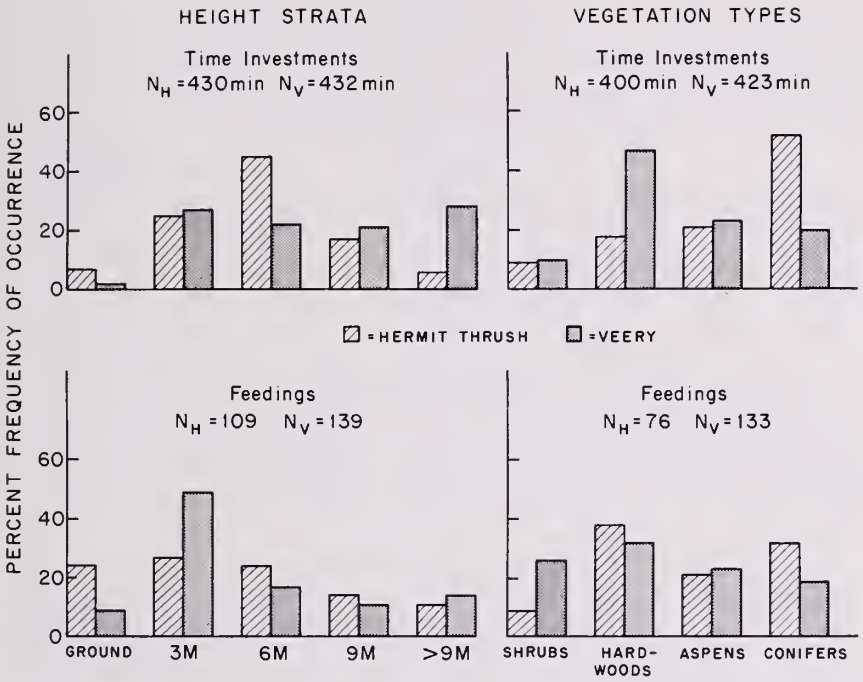

FIG. 1. The distribution of time investments and feedings among five height strata and four vegetation types for the Hermit Thrush and Veery.

outcome. I recognized the following prey capture methods in the vegetation: (1) glean—the bird hopped toward and then picked prey from foliage or woody stem while perched; (2) hover—the bird flew toward and captured prey located on foliage or woody stem; (3) hawk—the bird captured prey in mid-air; and (4) trunk-pounce—the bird flew toward prey located on a vertical surface, usually a tree trunk. The bird contacted the surface with its feet; clinging for a few seconds, it picked off the prey then resumed flight. The first three methods generally follow the terminology used by Robinson and Holmes (Ecology 63:1918–1931, 1982). The fourth method, trunk-pounce, is a distinct behavior frequently used by thrushes, including the American Robin (*Turdus migratorius*).

I also recorded the thrushes' foraging methods and feeding frequencies on the forest floor. Terrestrial travel involved short hops and runs. Prey captures consisted of ground gleans and probes (Holmes et al., Ecology 60:512–520, 1979).

Besides prey capture methods, I used movement rates and the distance of feeding moves, compared across arbitrarily determined length categories, to characterize the thrushes' foraging behavior. I used the distribution of intermove time intervals, based on 0.10-min categories, to compare the two species movement rates in the vegetation. Similarly, I recognized four categories in analyzing length distributions for the two species' feeding moves: 0–3 m, 3–6 m, 6–9 m, and >9 m.

Chi-square tests were used to analyze vegetational and behavioral data (Siegel, Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill, New York, New York, 1956).

Macrohabitat use and structure.—The two thrushes occurred in stands of second-growth

TABLE 3

SUMMARY OF HERMIT THRUSH AND VEERY FORAGING BEHAVIOR IN VEGETATION

	Movement patterns			
Species	N	Median rates of movement (moves/min) (upper boundary of 1st, 3rd quartiles)	N	Median feeding move lengths (m) (upper boundary of 1st, 3rd quartiles)
Hermit Thrush	334	3.8 (1.3, 11.1)	73	3.0 (0.6, 4.6)
Veery	550	3.6 (1.7, 10.0)	109	4.6 (1.0, 7.6)

	Frequency distribution of prey capture methods				
Species	N	% Glean	% Hover	% Hawk	% Trunk-pounce
Hermit Thrush	81	19	54	17	10
Veery	137	22	49	16	13

forest containing both deciduous and coniferous trees (Table 1), with sapling aspens being most abundant. Over half of both species' territories were covered by an overstory with a maximum height of about 20 m. A well-developed understory of bracken ferns (*Pteridium aquinlinum*), shrubs, and tree seedlings extended from the ground to 3 m on over 80% of the area contained in thrush territories.

Vegetation sampling (Table 2) revealed no significant differences ($P > 0.05$) between the two species territories in the distribution of tree types ($\chi^2 = 0.22$, df = 2, NS), tree sizes ($\chi^2 = 4.76$, df = 2, NS), overstory structure ($\chi^2 = 1.27$, df = 3, NS), or understory structure ($\chi^2 = 4.16$, df = 3, NS).

A simple macrohabitat difference between coniferous and deciduous vegetation did not separate the Hermit Thrush and Veery on my study sites. Both species occupied what Dilger (1956b) termed "disturbed coniferous forest." Co-occurrence of the Hermit Thrush and Veery in the same macrohabitat is not unusual (Dilger 1956b, Morse 1971, Holmes et al. 1979). In Maine, the two species chiefly occupy opposite ends of the forest moisture gradient, with Hermit Thrushes nesting in dry pine-oak stands and Veeries nesting in damp deciduous woodlands (Morse 1971). However, both species occur in some mesic, mixed conifer-hardwood stands that, based on Morse's description, appear to be similar to my sites.

Microhabitat use patterns.—The Hermit Thrush and Veery differed significantly in their distribution of time spent among the five height strata ($\chi^2 = 110.10$, df = 4, $P < 0.001$; Fig. 1). Total time spent on the ground by Hermit Thrushes was over three times greater than that spent by Veeries. Hermit Thrushes concentrated their activities in the two lower strata of vegetation, while Veeries spent time evenly among the height categories.

The species' feeding patterns also differed significantly with respect to height ($\chi^2 = 19.61$, df = 4, $P < 0.001$; Fig. 1). Hermit Thrushes did about one-quarter of their feeding on the forest floor, whereas ground feedings accounted for less than one-tenth of the prey captures observed for Veeries. Within the vegetation, both species fed chiefly below 6 m, but it was the Veery that concentrated on the lowest stratum.

The thrushes' time investment patterns support my predictions. The Hermit Thrush appeared more terrestrial and was active most commonly in the lowest forest growth. In

contrast, the Veery appeared to be more arboreal, ranging throughout the canopy, and thus potentially encountering a different set of prey and avian competitors (Dilger 1956b). However, territorial defense may have influenced vertical patterns in the vegetation more strongly than food resources (Morse, Ecology 49:779–784, 1968; Williamson, Ecol. Monogr. 41:129–152, 1971). The divergent time investments reflect differences in song sites. Hermit Thrushes concentrated their singing in the 6 m stratum (57% of observations), while Veeries sang most frequently at >9 m (46%).

Actual feeding patterns suggest a less distinct vertical separation between the species. Despite the fact that Hermit Thrushes foraged on the ground more than Veeries, terrestrial feeding was relatively uncommon in both species. Holmes et al. (1979) observed that both Hermit Thrushes and Veeries did over 40% of their foraging on the forest floor of the old-growth hardwood stands at Hubbard Brook, New Hampshire. Based on my continued observations, I think that ground foraging is infrequent at my study sites, perhaps because the dense ground cover of the second-growth forest presents conditions less amenable to this activity (Smith, Behaviour 48:276–302, 1974). However, when ground foraging does occur, movement and feeding rates are high. While Hermit Thrushes spent only 8% of their time on the forest floor, ground foraging produced 24% of all prey captures.

Within the vegetation the Veery, as well as the Hermit Thrush, fed principally in the forest understory and midstory (Fig. 1). However, shrubs served as the most important foraging site for Veeries in the understory (52% of feedings in 3 m stratum), whereas saplings and low tree growth were more important for Hermit Thrushes (79% of feedings). This relationship illustrates the role of both vegetation type and height in the partitioning patterns exhibited by the two thrushes within their common macrohabitat.

The two species differed significantly in their distribution of time investments among the four vegetation types ($\chi^2 = 10.77$, df = 3, $P < 0.02$). Hermit Thrushes spent more time in conifers while Veeries concentrated their activities in hardwoods (Fig. 1). Significant differences also existed between the thrushes' distributions of feedings among the vegetation types ($\chi^2 = 110.88$, df = 3, $P < 0.001$). Hermit Thrushes fed more in conifers; Veerys fed more in shrubs (Fig. 1). Both species made little use of aspens, relative to these trees' abundance in the environment.

Habitat partitioning based on differential use of broadleaf and coniferous trees is a common pattern among insectivorous birds (Klopfer, Behavioral Aspects of Ecology, Prentice-Hall, Engelwood Cliffs, New Jersey, 1962; Morse, Ecology 54:346–355, 1973; Partridge, Anim. Behav. 24:534–544, 1976). This pattern has been related to interspecific morphological differences, particularly differences in leg and bill structure, similar to those existing between the Hermit Thrush and Veery (Dilger 1956b, c). At my study site this partitioning mechanism operated within rather than between macrohabitats.

The Veery's frequent use of shrubs provides another source of segregation. Other studies (Dilger 1956b, Noon 1981) have reported that a well-developed shrub layer, such as commonly associated with disturbed woodland habitats, characterizes Veery territories.

Foraging behavior.—I expected the two thrushes to differ in their foraging behavior, based on differences in their morphology (Dilger 1956b, c) and their environment (Holmes and Robinson, Oecolgia 48:31–35, 1981). This was not the case. Hermit Thrushes did more ground foraging than Veeries, but as previously discussed, this behavior was used infrequently by both thrushes. The species did not differ significantly ($P > 0.05$) in their movement rates ($\chi^2 = 12.57$, df = 10, NS), feeding move lengths ($\chi^2 = 2.55$, df = 3, NS), or prey capture methods ($\chi^2 = 4.42$, df = 3, NS) in the vegetation (Table 3).

The behavior of both thrushes in the vegetation (Table 3) was intermediate between that of sit-and-wait species (e.g., the Olive-sided Flycatcher [*Nuttallornis borealis*] and Cassin's Kingbird [*Tyrannus vociferans*] [Eckhardt 1979; Landres and MacMahon, Auk 97: 351–365, 1980]) and widely foraging species (e.g., the Yellowthroat [*Geothlypis trichas*] and

Blackpoll Warbler [*Dendroica striata*] [Eckhardt 1979; Sabo, Ecol. Monogr. 50:241–259, 1980]). Noon (1981) suggested that the Veery was less well-adapted for and less dependent on true aerial prey captures, when compared to the most arboreal *Catharus*, Swainson's Thrush (*C. ustulatus*), because of the higher vegetation densities typical of Veery habitats. Veery and Hermit Thrush foraging was dominated by foliage-directed prey captures requiring flight and resembled the foraging strategy employed by other midstory species, such as tanagers (*Piranga* spp.) and small tyrant flycatchers (*Empidonax* spp.), which Robinson and Holmes (1982) termed "open-perch searching" (Williamson 1971, Eckhardt 1979, Holmes et al. 1979).

Frakes and Johnson (Condor 84:286–291, 1982) reported a parallel case of convergence in foraging behavior for two *Empidonax* flycatchers. These species typically occupied separate macrohabitats and displayed distinct foraging patterns, but where they co-occurred in intermediate environments, their foraging proved very similar. Habitat structure apparently plays a role in determining foraging strategy independent of interspecific interactions (Maurer and Whitmore, Wilson Bull. 93:478–490, 1981; Seidel and Whitmore, Wilson Bull. 94:289–296, 1982).

Conclusions.—The Hermit Thrush and Veery at Trout Lake were similar both at the level of macrohabitat structure and the level of foraging behavior. The clearest evidence for resource partitioning occurred at the level of microhabitat use, with the thrushes differing significantly in their overall activity and feeding patterns among height strata and vegetation types within their shared macrohabitat.

My observations support the general premise that large scale separations among similar species along particular resource axes, e.g., prey type or habitat type, should have their evolutionary origins in smaller scale differences among co-occurring local populations (Wiens and Rotenberry, Ecol. Monogr. 50:287–308, 1980).

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Interspecific song learning in a wild Chestnut-sided Warbler.—Vocal learning involving imitation is the prevalent mode of song development in songbirds. The evidence for vocal learning both from experimental studies and from local song variants shared among neighbors (dialects) indicates that songbirds generally learn from their own species, and that a genetically determined signal recognition center ("auditory template") constrains song learning within the species (Marler, *in* Function and Evolution in Behaviour, Baerends, Beer, and Manning, eds., Clarendon Press, Oxford, 1975; Payne, Auk 97:118–134, 1980; Marler and Sherman, J. Neuroscience 3:517–531, 1983). However, an increasing number of field and experimental studies have shown instances where birds learn the song of other species (Baptista, Z. Tierpsychol. 30:266–270, 1972; Wilson Bull. 93:265–267, 1981; Baptista and Morton, Auk 98:383–385, 1981; Eberhardt and Baptista, Bird-Banding 48:193–205, 1977; Kroodsma et al., Wilson Bull. 95:138–140, 1983). Evidence of vocal learning in the Parulinae (wood warblers) comes from one experimental Chestnut-sided Warbler (*Dendroica pensyl-*

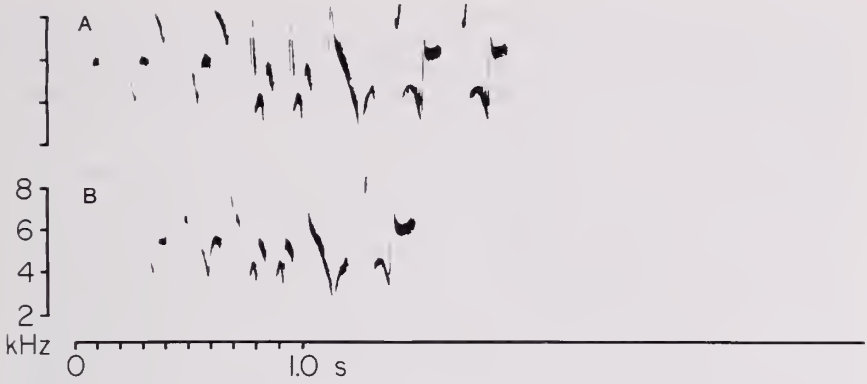

FIG. 1. A. Song of a wild Indigo Bunting XSOW at Niles, Cass Co., Michigan, recorded 24 May 1983. B. Song of a wild Chestnut-sided Warbler recorded at Niles, Cass Co., Michigan, 8 June 1983. The song-figures (notes) and their sequence are nearly identical in the two birds, but the phrasing of the song elements is more rapid in the warbler. All song-figures and their sequence are characteristic of a local song dialect of the buntings.

vanica) that imitated parts of the tutor songs of a Common Yellowthroat (*Geothlypis trichas*) and from a wild Common Yellowthroat that had a nearly perfect match of a song of a Chestnut-sided Warbler (Kroodsma et al. 1983). Observations of matching songs among neighboring wild males provides field evidence that wild Chestnut-sided Warblers develop their songs by imitative learning (Kroodsma, Auk 98:743–755, 1981).

We observed a wild Chestnut-sided Warbler near Niles, Cass Co., southern Michigan, with a song that was a nearly perfect match of local Indigo Buntings (*Passerina cyanea*). The bird sang at the edge of a secondary mesic woodland bordering McKinzie Creek in habitat with sugar maples (*Acer saccharum*), elms (*Ulmus* sp.), and willows (*Salix* sp.) about 10 m high, and dense shrubs along the woodland edge. At 07:45 on 31 May 1983, LLP recorded a bird singing a bunting song that differed from individual buntings known to live in the woods. While the bird was being recorded, it was seen and identified by LLP and SMD as an adult male Chestnut-sided Warbler. At 07:10 on 8 June the circumstances from the May encounter were repeated 120 m away by RBP and SMD. The bird sang in a bare tree in full view with its bill opening wide with each song. In neither instance did the two Indigo Buntings on this warbler territory respond to the warbler.

Comparison of audiospectrograms of the warbler's song with that of local Indigo Buntings indicated that the warbler had the same song (that is, the same sequence of song-figures) as eight male buntings located 0.8–1.1 km to the east of the warbler (Fig. 1). Indigo Bunting neighbors commonly match songs with each other (Payne et al., Behaviour 77:199–221, 1981; Payne, Anim. Behav. 31:788–805, 1983). All 17 warbler songs were identical with respect to their song-figures, sequence, and timing. The warbler's song was delivered more rapidly than those of the buntings because four out of five of the time intervals between song-figures of the warbler were of shorter duration than the intervals between the same figures in the bunting song. In its timing the song tended to resemble the normal, faster-paced song of wild Chestnut-sided Warblers. The precise matching of bunting song-figures and their sequence indicated that the warbler had copied the song of the local Indigo Buntings. The warbler's song consisted of two paired song-figures followed by two more song-figures,

each given only once (Fig. 1B). Most of the eight buntings that sang this song regularly paired each of these four different figures. Only one bunting, banded XSOW, sang the second from the last song figure without repetition (Fig. 1A). No buntings were recorded singing the last song figure singly as the warbler did. It appears that the Chestnut-sided Warbler copied XSOW, an adult bunting who has been at the study area for at least 3 years. The song may have been copied early in 1983 (XSOW was first seen in 1983 on 24 May) or in an earlier year. Although additional Chestnut-sided Warblers were observed on the study area regularly during the breeding seasons from 1978–1983, none were heard singing unusual songs.

The context of singing suggests that the copied song may have been used by the warbler as an "Accented Ending" song. Chestnut-sided Warblers have two main classes of song, Accented Ending and Unaccented Ending (Lein, Can. J. Zool. 56:1266–1283, 1978; Kroodsma 1981). Accented Ending songs tend to be sung more frequently early in the season and before the male is mated. No mate or nests were found for the warbler and the warbler was not seen or heard on this territory later in the season. The structure of the song differs from both the Accented Ending and Unaccented Ending songs in the details of the terminal notes that define the song classes. In certain features the form of the terminal song figure resembles the penultimate song figure in the Accented Ending type 2 of a warbler song neighborhood (Lein 1978: Fig. 2). The penultimate song figure resembles a warbler note recorded by Lein (1978: Fig. 4f, 6a, middle notes) in some Unaccented Ending songs.

The observation of interspecific song learning by a Chestnut-sided Warbler of a local song of an Indigo Bunting suggests that song development in this species is not tightly constrained by an innate predisposition to learn only species-same behaviors. The warbler's faster delivery of the bunting song-figures may, however, reflect a species-specific constraint in the same manner as Greenfinches (*Carduelis chloris*) copying Canaries (*Serinus canarius*) retain Greenfinch-specific interval timing (Güttinger, Z. Tierpsychol. 49:285–303, 1979). The closer match of the wild warbler's song with the apparent tutor's song than was observed in the experimental Chestnut-sided Warbler (Kroodsma et al. 1983) is consistent with the suggestion that song learning in birds may normally depend upon social interaction (Baptista and Morton 1981, Kroodsma 1981, Payne 1983). The circumstances in which the warbler copied the bunting song may have involved aggressive social interaction; the two species overlap in habitat and both nest in shrubs below 1 m. The bunting may also have caught the ear of the warbler at a critical period in its behavioral development. Whether song development in the warbler involved response to the similar acoustic features of songs of the two species, or to social interaction, or both, is unknown.

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An apparent hybrid Black-billed × Yellow-billed Cuckoo.—On 22 October 1974, R. Miller, Meridian, Butler Co., Pennsylvania, found a dead cuckoo and took it to the taxidermy laboratory of Carnegie Museum of Natural History, then located in Meridian. It was prepared as a study skin by O. M. Epping, and eventually delivered to the museum in Pittsburgh. Superficially similar to a Yellow-billed Cuckoo (*Coccyzus americanus*), it was catalogued (CM 149972) into the museum collection as a member of that species. It was sexed as a male; no notes were made by the preparator about fat or molt, but the specimen has obvious

pinfeathers on the forehead and throat. The bird was apparently just completing its first prebasic body molt.

While examining immature *Coccyzus* specimens recently, I was struck by several color anomalies in the Meridian specimen. Further study indicated that this specimen is probably a hybrid between the Yellow-billed Cuckoo and the Black-billed Cuckoo (*C. erythropthalmus*).

First-year *Coccyzus* cuckoos are readily distinguishable from adults by the narrowness of their rectrices, and the Meridian specimen clearly belongs to this age class. It was compared with nine first-year specimens of each species. In young Yellow-billed Cuckoos the rectrices (except the central pair) are dull black or dark gray above, with well defined broad white or grayish white tips on the outer three pairs. The outer two pairs also have a sharply defined whitish margin on the outer web. Black-billed Cuckoos of the same age class have olive-brown rectrices with no more than a small dull white spot at the tips. The outer edge of the outer two pairs has a very narrow (<0.5 mm), inconspicuous pale margin. In the Meridian specimen the rectrices are dark gray as in the Yellow-billed Cuckoo, but duller and browner; the terminal spots are as large as in that species but are not clearly defined at the proximal edge, blending more gradually into the dark gray area. Similarly, white outer margins are present on the outer two pairs of rectrices, but these are not clearly defined as in the Yellow-billed Cuckoo.

Neither the Yellow-billed Cuckoo nor the Black-billed Cuckoo normally replaces rectrices at the time of the first prebasic body molt in the fall (Bent, U.S. Natl. Mus. Bull. 176, 1940). In the Meridian specimen, the left outermost rectrix is sheathed at the base and has grown to about ⅔ of full length. This undoubtedly represents replacement of an accidentally lost rectrix. The new feather is of adult shape and color, although rectrices of this kind would not normally be grown until some months later. The color and pattern of the new feather in the Meridian specimen are essentially those of the Yellow-billed Cuckoo, except that in that species the white tip is sharply defined from the adjacent black of the rest of the feather, whereas in the Meridian specimen the pigmentation fades from black to white in a band about two mm wide along this border.

The anterior underparts of young Black-billed Cuckoos are buffy-gray; in Yellow-billed Cuckoos this area varies from pure white to a purer, less buffy gray than in the black-bill. In the Meridian specimen the anterior underparts are lightly washed with a buffy-gray similar to that of the Black-billed Cuckoo. In the Yellow-billed Cuckoo the flanks are white, lightly washed with buff or gray, and the under tail coverts are usually white, sometimes cream. In the Black-billed Cuckoo the flanks are buffy-gray like the breast, and the under tail coverts are distinctly buffy. These areas in the Meridian bird are like the Black-billed Cuckoo but somewhat paler.

One of the most conspicuous differences between these two species of cuckoo is the color of the wings in dorsal aspect. In the Yellow-billed Cuckoo the inner webs of the primaries are strongly rufous on the proximal half; there is a rufous tinge to the proximal portion of the outer webs of the primaries and outer secondaries, and all of the wing coverts have rufous margins. Young Black-billed Cuckoos lack the rufous on the inner webs of the remiges, which are white to pale buff. They tend to have some rufous on the outer webs of the inner primaries and outer secondaries (lacking in adults), duller than that of the Yellow-billed Cuckoo, and a highly variable amount of the same dull rufous edging on some of the wing coverts. In the Meridian bird the wings, in general, are like those of the Yellow-billed Cuckoo, but the greater coverts lack rufous edgings, contrasting abruptly with the reddish primary coverts.

The bill color from which the two species take their English names is also diagnostic. In the Yellow-billed Cuckoo the lower mandible is bright yellow on the proximal ¾, as is the

area of the upper mandible below the nostrils. This area remains yellow in museum specimens as much as a century old, clearly contrasting with the dull black of the remainder of the bill. In young Black-billed Cuckoos, the lower mandible varies from the black of the upper mandible to blue-gray in color. In those examples whose lower mandibles were blue-gray in life, the color fades to white in museum specimens. In the Meridian bird, the lower mandible is yellowish brown, contrasting much less with the upper mandible than in Yellow-billed Cuckoos, and darker than any museum specimen examined of the latter species. It is thus intermediate between the yellow lower mandible of Yellow-billed Cuckoos and the black (rather than blue-gray) extreme of lower mandible color in young Black-billed Cuckoos.

The measurements presented by Ridgway (U.S. Natl. Mus. Bull. 50, Pt. 7, 1916) indicate that adult Black-billed Cuckoos have, on the average, shorter wings and bills but longer tails than adult Yellow-billed Cuckoos. The sexes are alike in size. First-year specimens measured for this study (as mentioned, nine of each species) confirm all except the tail differences; there was no significant difference in tail lengths between the two series, and the Yellow-billed Cuckoo series included both the longest- and shortest-tailed specimens. The measurements (mm) were as follows: flattened wing—Black-billed Cuckoos 128.5–141 (134.5), Yellow-billed Cuckoos, 140–152.5 (145.0), hybrid 142; tail—Black-billed Cuckoos, 134–150 (142.8), Yellow-billed Cuckoos 132–161 (143.9), hybrid 136; bill from anterior end of nostril—Black-billed Cuckoo 15–19.5 (17.1), Yellow-billed Cuckoos 18–20 (18.7), hybrid 17.5. The hybrid thus has a wing length like that of a large Black-billed Cuckoo or small Yellow-billed Cuckoo, a tail length within the range of both species, and a bill length like an average Black-billed Cuckoo or a very small Yellow-billed Cuckoo. In all other characters (color, pattern), the Meridian specimen is essentially intermediate between the two species, although more like the Yellow-billed Cuckoo in tail, wing and bill color and more like the Black-billed Cuckoo in underparts color.

Hybridization is apparently rare in the family Cuculidae. None has been reported prior to my describing a hybrid Philippine Coucal (*Centropus viridis*) × Lesser Coucal (*C. bengalensis*) (Parkes, Living Bird 4:94–95, 1965). I know of no other record of hybridization between the Yellow-billed and Black-billed cuckoos, which are widely sympatric in North America. Each of these species of *Coccyzus* is known occasionally to lay eggs in the nest of the other (several references given by Bent 1940:56). It is tempting to speculate that one of the parents of the Meridian bird hatched from such a misplaced egg and was thus imprinted on the wrong species.—KENNETH C. PARKES, *Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213.* *Accepted 15 Feb. 1984.*

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Clutch-size and nest placement in the Brown-headed Nuthatch.—Brown-headed Nuthatches (*Sitta pusilla*) occupy southeastern pine forests from eastern Texas to Florida, north to Arkansas and the southern tip of Delaware; an insular race occurs on Grand Bahama Island (A.O.U. Checklist 1983). Data on their nesting biology are scattered except for that collected by Norris (Univ. Calif. Publ. Zool. 56:119–300, 1958). Information on clutch-size, nest placement, and other aspects of nesting biology throughout the species' range is available on oology cards and in the literature. Collation and study of data from these sources has allowed me to quantitatively examine some facets of Brown-headed Nuthatch breeding biology.

Methods.—I requested oology data from various museums and used a total of 372 cards. In addition, I conducted a literature search for nesting records (N = 35), received Cornell Nest Record Card Program (NRCP) data (N = 22), and solicited information from indi-

viduals. Most nests were only visited once, and I treated all data having complete egg sets accordingly. The date of clutch initiation was determined by a procedure similar to that of Anderson and Hickey (Wilson Bull. 82:14–28, 1970). (For data in the literature and from the NRCP, I followed the method of Myres, Bird Study 2:2–24, 1955.) The egg sets were arranged into five groups depending on estimates of the length of time they had been incubated. The estimated date of clutch initiation was equal to the date the egg set was collected minus clutch-size plus 1 day; additional days were then subtracted from these dates according to the collector's estimation of incubation time elapsed: fresh = 2, slight = 4, advanced = 10, unknown = 7 (half of incubation period). If the number of days of incubation had been estimated and stated explicitly, I used that number. This fifth group then overlaps groups one through four. Clutch-size, estimated by nestling sets, was significantly lower than estimates of clutch-size by egg sets ($t = 3.57$, N = 369/20, $P < 0.01$), and thus, nestling set data were not used.

Average clutch-size was calculated from clutches containing no fewer than three eggs. Smaller clutches were assumed to be incomplete and were not used in the analysis; this involved fewer than 15 nest records. This assumption is supported by accounts in Bent (U.S. Natl. Mus. Bull. 195, 1948), Norris (1958) and others.

Results.—An analysis of variance was performed comparing the five incubation-stage groups with respect to both the date of clutch initiation and clutch-size. I found no significant differences among any of the five incubation groups with respect to either the date of clutch initiation or clutch-size. Accordingly, I pooled data on date of clutch initiation and clutch-size from all incubation groups.

The majority of nest records are from coastal regions of Florida, Georgia, North Carolina, and South Carolina. The mean egg date for all states in the range of the Brown-headed Nuthatch is 9 April ± 19 days (SD) (median = 7 April), as suggested in the literature (Howell, Florida Bird Life, Coward-McCann, New York, New York, 1932; Burleigh, Birds of Georgia, Univ. Georgia Press, Athens, Georgia, 1958; Norris 1958; Oberholser, The Bird Life of Texas, Vol. II, Univ. Texas Press, Austin, Texas, 1974; Haney, Migrant 52:77–86, 1981; and others). The egg-laying period spanned approximately 2 months within each state and 90% of all clutches were laid before 5 May. The onset of breeding began rapidly around 10 March and the distribution of egg dates was slightly skewed to the right. There are six records of renesting attempts and two records of second broods. Several late records extended into mid-July (Coffey, Chat 7:77, 1943; six eggs, incubation fresh, Chatham County, Georgia, 20 July 1925, collected by T. D. Perry). There are no significant differences with respect to mean egg date among Florida, Georgia, and South Carolina; in those states, mean egg date ranged from 4–6 April ± 17–20 days (SD). The mean egg date in North Carolina was 23 April ± 16 days (SD), which is significantly different from the other three states (ANOVA, $F = 13.22$, $P < 0.005$). I also tested for differences in mean egg date among latitudes (range = 27–38°N), when egg dates are grouped according to 1°-latitudinal increments. I found no significant differences in mean egg date of any one latitude in pairwise comparisons with all other latitudes, i.e., no single latitudinal group stood alone, apart from all the others, though there are several homogeneous subsets (ANOVA, $F = 10.56$, $P < 0.005$; Student-Newman-Keuls test).

The mean clutch-size for all states is 5.10 ± 0.91 (SD) (N = 369). Clutch-size ranged from three to seven and I included one record of a clutch of nine (Arnow, Auk 24:447, 1907). The modal clutch-size throughout the brownhead's range is five (146 nests, 39.6%) and the next most frequent is six (115 nests, 31.2%), except in Florida where the first and second most common clutch-sizes are four and five. There is a significant positive correlation between clutch-size and latitude ($r = 0.29$, $P < 0.005$) and a significant negative correlation between clutch-size and date of clutch initiation ($r = -0.18$, $P < 0.005$). Compared to all

TABLE 1
CLUTCH-SIZE OF THE BROWN-HEADED NUTHATCH

State	N	$\bar{x} \pm$ SD
Florida	80	4.50 ± 0.80[a]
Georgia	96	5.17 ± 0.90
South Carolina	90	5.38 ± 0.76
North Carolina	61	5.11 ± 0.90
All other states (N = 9)	42	5.43 ± 1.00

[a] Homogeneous subsets, Student-Newman-Keuls test.

other states, only Florida had a significantly smaller mean clutch-size (ANOVA, $F = 14.23$, $P < 0.005$; Student-Newman-Keuls test; Table 1) and this is also true when adjusted for date of clutch initiation. When clutch-size data from Florida were removed, there was no significant correlation of clutch-size with latitude ($r = 0.01$, $P > 0.05$). I also tested for differences in mean clutch-size among latitudes, when latitudes were grouped according to 1°-latitudinal increments. I found no significant differences in mean clutch-size of any one latitude in pairwise comparisons with all other latitudes, i.e., no single latitudinal group stood alone, apart from all the others, though there are several homogeneous subsets (ANOVA, $F = 7.44$, $P < 0.005$; Student-Newman-Keuls test).

The incubation period for Brown-headed Nuthatches, as measured from the last egg laid to the last egg hatched, is given as 14 days (Grimes, Florida Nat. 6:8–13, 1932; Bent 1948; Beers, Chat 16:78–80, 1952; Quay, Chat 19:87–88, 1955; Norris 1958). The mean nestling period is about 18.5 days (Bent 1948, Norris 1958). Nestling periods of 18–19 days (Norris 1958; Norwood, Chat 23:82, 1959), 19 days (Draper—observer, Guilford County, North Carolina, 1973, from NRCP), 19–20 days (Norwood, Chat 20:73–74, 1956), 20 days (Beers 1952, Norris 1958), and 23 days (Norwood, Chat 19:19–20, 1955) have also been recorded. These longer nestling periods involved pairs breeding later than usual, renesting attempts, or second broods after successful fledging of a first clutch.

Double-brooding by Brown-headed Nuthatches has been documented by Norwood (1956, 1959) and claimed by Becket (*in* Sprunt and Chamberlain, revised by Burton, South Carolina Bird Life, Univ. South Carolina Press, Columbia, South Carolina, 1970). Nicholson stated (on oology slip with egg sets) that brownheads may rear two broods in Flagler County, Florida, as did Baynard (Auk 30:240–247, 1913) for Alachua County, Florida. Possible double-broodedness was recorded in Atlanta, Georgia (Eyles and Giles, Auk 52:462, 1935) and in North Carolina (comment on oology slip with egg sets collected by T. A. Southwick).

Nest-sites were grouped into 12 categories (Table 2). Nests were found in various conifers including longleaf (*Pinus palustris*), slash (*P. elliottii*), loblolly (*P. taeda*), pond (*P. serotina*), shortleaf (*P. echinata*), sand (*P. clausa*) and Virginia (*P. virginiana*) pines, baldcypress (*Taxodium distichum*), and Atlantic white-cedar (*Chamaecyparis thyoides*). Hardwood trees containing nests included willow (*Salix* spp.), poplar (*Populus* spp.), pecan (*Carya illinoensis*), oaks (*Quercus* spp.), sycamore (*Platanus occidentalis*), sweetgum (*Liquidambar styraciflua*) (most frequent hardwood used), pear and apple (*Pyrus* spp.), peach (*Prunus persica*), prickly-ash (*Xanthoxylum* spp.), holly (*Ilex* spp.), black tupelo (*Nyasa sylvatica*), dogwood (*Cornus* spp.), ashes (*Fraxinus* spp.), and *Catalpa* spp. The modal cavity height for all nest-site categories was 1.2 m (17.4%). The median cavity height was 1.5 m. The cavity height distribution was strongly skewed toward higher cavity heights (mean height

TABLE 2
NEST-SITE LOCATION AND CAVITY HEIGHT (M)

Nest-site	N	$\bar{x} \pm SD$
Pine trunk	22	3.78 ± 2.65
Stump	144	1.86 ± 1.34
Limb	1	9.15 —
Deciduous trunk	7	3.69 ± 2.14
Stump	21	2.17 ± 1.04
Limb	1	3.05 —
Nest box	15	1.80 ± 0.34
Post	39	1.25 ± 0.55
Pole	4	4.82 ± 1.01
Tree unidentified	6	3.75 ± 2.29
Stump unidentified	45	1.86 ± 1.25
Other nest-sites	4	4.27 ± 1.20
Total	309	2.09 ± 1.59

of 2.1 m ± 1.6 SD). Ninety percent of all cavity heights recorded were below 3.66 m. The lowest nests recorded included one at 15 cm (Wayne, Birds of South Carolina, Contrib. Charleston Mus. No. 1, 1910), one at 30 cm (Sprunt, in litt.), and five at 45 cm in fence posts and pine stumps. Wayne (1910) recorded a cavity at 27.5 m. Nest-sites in pine stumps, deciduous stumps, unidentified stumps, posts, and nest boxes, with nesting cavities located at mean heights of less than 3 m, are most frequently used. All other nest-sites, with cavities at mean heights of greater than 3 m, were infrequently used, except for pine trunks (Table 2). These results on nest placement agree with the literature (Bent 1948, Norris 1958, and others).

Secondary cavities are rarely used. There were some records of nests in nest boxes (N = 20; see also Table 2) and natural cavities (N = 24). There are also single records of brownhead nests in an old Downy Woodpecker (*Picoides pubescens*) hole in a limb of a yellow pine (St. Marys County, Maryland) and in an abandoned woodpecker hole in a cypress fence post (Orange County, Florida).

Unusual nest-sites used by Brown-headed Nuthatches have been recorded. A cavity was dug in the side of a 7.5-cm plank leaning against a tree in open pine woods at Savannah, Georgia (Burleigh 1958). Fire scar depressions in old pines have been used and naturally occurring cavities under bark have been used without excavation (at least 12 records). A hole 0.6 m above the ground in a railroad crosstie (Hopkins, The Birdlife of Ben Hill County, Georgia, Occ. Publ. No. 5, Georgia Ornithol. Soc., 1975), a cavity in a decayed pole of a timber boom in a bayou, holes in wooden pilings, wooden street sign posts, and other natural cavities of pine and fence posts have also been used. Brownheads frequently select nest-sites in clearcuts, along roadsides, in windbreaks, over ponds, and in fields. Burleigh (1958) found a nest in a fence post in a field 460 m from the nearest woods.

Brownheads may start several excavations before finishing the eventual nest cavity (Bent 1948, Norris 1958, many egg collectors in litt.). Since they usually excavate their own nest, partially rotted wood is a prerequisite. The sapwood is excavated from between the bark and heartwood, and the cavity often follows the outline of impenetrable heartwood (May,

Bird-Lore 27:383–386, 1925; Norris 1958). Cracks and crevices in the nest cavities are plugged up with bark shreds (Nicholson, in litt.; several other records). Pine stumps and posts, particularly those with bark attached, are favored (Table 2). Cedar, especially unshaven cedar posts with bark attached, are also among preferred nest-sites for brownheads.

Cavities are usually long, narrow, and irregular in size and shape. The largest natural cavity size recorded was 10.2 × 10.2 × 20.3 cm. Most nest boxes had larger dimensions. The largest was 14.0 × 12.7 × 20.3 cm. Cavity depth was measured from the bottom of the cavity entrance to the bottom of the cavity (N = 69). Values ranged from 7.6–40.6 cm with most of the total ranging from 12.7–25.4 cm, with modes of 15.2 and 20.3 cm. This agrees with the literature (Wayne 1910, Bent 1948, Burleigh 1958, Norris 1958, and others). The cavity entrance is often jagged, sometimes circular, with most diameters ranging from 2.5–3.8 cm (N = 34). Only five entrances were greater than 3.8 cm in diameter, from 3.8–5.1 cm. These latter measurements agree with values of the diameter of the cavity entrance provided by Norris (1958).

Eastern Bluebirds (*Sialia sialis*) are the Brown-headed Nuthatch's most frequent competitors for cavities (Barefield, Raven 14:34–37, 1943; Bent 1948; Hearne, Chat 13:78, 1949; Oliver, Oriole 17:17, 1952; Houck and Oliver, Auk 71:330–331, 1954; Norris 1958; several other records, in litt.). Brownheads may also be aggressive toward woodpeckers during excavation, nest-building, and incubation (Beers 1952; Norris 1958; several other records, in litt.). Woodpeckers occasionally destroy nuthatch eggs and young. Interspecific competition at nest-sites between brownheads and other species have been recorded, as have interspecific coexistence with other species, including bluebirds and woodpeckers (Coffey 1943, Norwood 1956, Norris 1958, Haney 1981). The majority of cavity interactions between brownheads and bluebirds or other species were at atypical nest-sites (high cavity heights, deciduous trees, tree limbs, nest boxes) and less preferred habitat (suburbia).

Discussion.—The fact that mean date of clutch initiation and mean clutch-size were not significantly different when the five incubation-stage groups were compared suggests that oologists are usually able to judge correctly the incubation stage of any nest. Thus, oologists' methods of estimating the incubation stage are not believed to seriously bias determination of the date of clutch initiation or clutch-size. I did not explicitly compare oology data to more recent data collected from the Cornell NRCP, the literature, and several individuals, because of the small sample sizes of the latter sources. Several other nest record studies have pooled the latter sources with oology data without indicating or suggesting the existence of significant differences between the different sources (Von Haartman, pp. 611–619 *in* Proc. 13th Inter. Ornithol. Congr., Oxford, England, 1963; pp. 155–164 *in* Proc. 14th Inter. Ornithol. Congr., Canberra, Australia, 1967).

Collation and study of data from the sources cited herein have clarified our knowledge of Brown-headed Nuthatch breeding biology with respect to date of clutch initiation, clutch-size, incubation period, double-broodedness, nest-sites, use of secondary cavities, cavity size and characteristics, and cavity competitors. In general, there is agreement between oology data and the literature on these facets of Brown-headed Nuthatch breeding biology. This is not surprising, for accounts in the literature are based, to a varying degree, on data from oologists. Lack of clearer differences among states of 1°-latitudinal increments with respect to mean date of clutch initiation or clutch-size may occur because of small sample-sizes or may be due to biases: uneven observer coverage with respect to time of year and locality, for example. Nevertheless, quantification of these parameters has improved our knowledge of them.

One important result, undocumented in the literature, is the significantly lower clutch-size in Florida compared to other states in the brownheads' range (Table 1). The significance of this is unknown. Lower mean clutch-size in Florida compared to other southeastern states or larger geographical areas has also been documented for Red-tailed Hawks (*Buteo jamai-*

censis) (Henny and Wight, Fish & Wildl. Serv., Wildl. Resear. Rept. 2:229–250, 1972), Eastern Bluebird (Peakall, Living Bird 9:239–255, 1970), and several other passerines (Crowell and Rothstein, Ibis 123:42–50, 1981). The significant decline in clutch-size with date of clutch initiation for Brown-headed Nuthatches conforms with the usual pattern observed in passerines (Lack, Ecological Adaptations for Breeding in Birds, London, England, 1968).

Acknowledgments.—I thank the following institutions for sending me oological data: Adams State College, Alamosa, Colorado; American Museum of Natural History; University of Arkansas; California Academy of Sciences; Carnegie Museum; Charleston Museum; Chicago Academy of Sciences; Clemson University; Cleveland Museum of Natural History; Cornell University; Cornell Laboratory of Ornithology; Delaware Museum of Natural History; Field Museum of Natural History; Florida State Museum; Florida State University; Illinois State Museum; University of Massachusetts; University of Miami, Florida; University of Michigan; Mississippi Museum of Natural Science, Jackson; Museum of Comparative Zoology, Harvard University; Museum of Science, Boston; Museum of Vertebrate Zoology, University of California, Berkeley; Montshire Museum of Science, New Hampshire; National Museum of Natural History, Smithsonian Institution; Ohio State University, Columbus; Peabody Museum, Yale University; Reading Public Museum, Pennsylvania; Royal Ontario Museum, Toronto; San Bernardino County Museum; University of South Florida; Strecker Museum, Baylor University; Tall Timbers Research Station, Florida; Washington State University; Western Foundation of Vertebrate Zoology, Los Angeles; William Penn Memorial Museum, Harrisburg; University of Wisconsin, Zoological Museum, Madison. I also thank the following individuals for sending data: J. H. Carter, III, D. M. Forsythe, and M. M. Hopkins, Jr. My study was partially supported by the Department of Biological Sciences, Mississippi State University, Mississippi, and by the Department of Biological Sciences, Clemson University, South Carolina. I thank F. C. James and H. Ross and the editorial staff of *The Wilson Bulletin* for constructive criticisms.—Douglas B. McNair, *Dept. Zoology, Clemson Univ., Clemson, South Carolina 29631.* *Accepted 27 Jan. 1984.*

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A record of ground nesting by the Hermit Warbler.—On 15 May 1979, a single Hermit Warbler (*Dendroica occidentalis*) ground nest was discovered 1.6 km west of Castella, Shasta Co., California. The nest, which contained five eggs, was located under the litter in a pocket formed by basal branching of a hazelnut (*Corylus cornuta*). Overstory vegetation consisted of Douglas-fir (*Pseudotsuga menziesii*) topped by California black oak (*Quercus kelloggii*).

An adult female was sitting on the nest at time of discovery and allowed one of us (CRM) to approach <1 m before she flew. She did not move far. Soon, a male bird flew in with a green caterpillar which he offered to his mate. The female, apparently preoccupied with the presence of the observer near her nest, declined the meal, and the male ate the caterpillar. A visit to the nest 2 days later revealed two newly hatched chicks and three eggs. No further visits were made to the nest.

We are unaware of any other records documenting ground nesting in the species, and our literature search included the North American Nest Record Program at Cornell's Laboratory of Ornithology. Cogswell (pp. 144–146 *in* The Warblers of America, Griscom and Sprunt, eds., The Devin-Adair Company, New York, New York, 1957) reported the nest is nearly always located in conifers, saddled on horizontal branches at moderate heights (6.1–12.2 m) but varying from 0.6–15.2 m.

We thank Chandler Robbins and Daniel Leedy for comments on this note.—Charles R. Munson and Lowell W. Adams, *National Institute for Urban Wildlife, 10921 Trotting Ridge Way, Columbia, Maryland 21044.* *Accepted 1 Dec. 1983.*

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El Niño and a brumal breeding record of an insular Savannah Sparrow.—Breeding by birds in temperate latitudes is usually confined to the spring and summer months. Aseasonal breeding may occur in a few individuals in areas with mild climates (review in Orians, Auk 77:379–398, 1960; Wells and Baptista, Western Birds 10, 83–85, 1979). Observations by ornithologists visiting the San Benito Islands, Baja California, suggest that breeding by the endemic subspecies of Savannah Sparrow (*Passerculus sandwichensis sanctorum*) is relatively synchronized and seasonal (Anthony, Auk 23:150, 1906; Thayer and Bangs, Condor 9:81, 1907; Boswall, Bristol Ornith. 11:29, 1978).

I visited West San Benito Island on 8 February 1983. Singing was sporadic among the abundant local population of Savannah Sparrows, and no obvious signs of breeding activity were noted. However, loud begging calls were heard when a Savannah Sparrow with insects in its bill disappeared into a bush. Two fledgling Savannah Sparrows were flushed from the bush, and one was caught and later released. Its distress calls attracted an adult Savannah Sparrow which alarm-called incessantly. The fledgling had a short tail, was hardly able to fly and must have recently left the nest.

J. Rising (in litt.) visited the San Benito Islands on 12 February 1983. He also noted that the Savannah Sparrows were not singing vigorously and saw one individual of a pair carrying food. Their behavior suggested that they had a nest in boxthorn-cholla thicket, although neither a nest nor fledged young could be found.

Incubation times reported for the Savannah Sparrow are 12 days for Maine (Palmer, Maine birds, Bull. Mus. Comp. Zool. 102, 1949), 12.2 days for Nova Scotia (Dixon, Auk 95:235–46, 1978), and 12 days for Michigan (Potter, Jack-Pine Warbler 52:50–63, 1974). Nestling life is reported to last 14 days in Maine, 9 days in Nova Scotia, and 8 days in Michigan (see refs. above). Assuming that the fledgling I found was about 8 days old, the clutch must have been completed about 19 January. The Mexican check-list (1957) gives one laying record for 6 February, apparently based on data from ovaries on two specimens from West San Benito Island deposited in the Museum of Vertebrate Zoology, Univ. California, Berkeley, by J. R. Hendrickson (MVZ 120279 and MVZ 120283). The specimens were taken on 6 February 1950. The labels indicated that one female had a 5-mm ovum and a second female had a 4-mm ovum. A third specimen had very small ova inscribed on the specimen label. These data suggest that although two of the females were ready to lay, laying may not have taken place yet, and should not be considered as reliable laying records.

Evidently most of the breeding activity takes place between March and June (see above). Dates were examined on 77 sets of Savannah Sparrow eggs in the collection of the Western Foundation of Vertebrate Zoology, Los Angeles, California. The earliest date for 46 sets of eggs from Mexican mainland populations (*P. s. anulus, P. s. guttatus, P. s. rostratus*) was 7 April. The earliest date on 31 sets of eggs of the insular *P. s. sanctorum* was 31 March. These data suggest that the breeding record for January reported herein is an exception and not the rule.

Nineteen eighty-three was an "El Niño" year bringing warm waters off the Baja California coast and much rain in January. The island vegetation which may be characterized as scrub-desert was quite green with herbaceous vegetation at the time of our visit. Dr. T. Walker, a frequent visitor on the island who accompanied me, informed me that the lush vegetation was unusual for that time of the year. Perhaps the brumal breeding record(s) of the Savannah Sparrow reported herein may be another consequence of the Niño.

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for helpful comments on an earlier draft of this manuscript and Kiff for data on egg sets from the Western Foundation of Vertebrate Zoology, Los Angeles, California.—Luis F. Baptista, *Dept. Ornithology/Mammalogy, California Academy of Sciences, San Francisco, California 94118. Accepted 11 Nov. 1983.*

Wilson Bull., 96(2), 1984, pp. 303–305

Age and reproductive success in Northern Orioles.—Rising (Syst. Zool. 19:315–351, 1970) reported breeding by first-year male Northern Orioles (*Icterus galbula*) but did not compare reproductive success of first-year and older males. I recently investigated various aspects of the breeding of first-year and older males in west-central Kansas (Labedz, M.S. thesis, Fort Hays State Univ., Hays, Kansas, 1982). Data concerning clutch-size, fledging success, and range of fledging dates are reported herein.

Methods.—Clutch-size, fledging success, and fledging dates were recorded from a 120-ha study area near Hays, Ellis Co., Kansas in 1981 and 1982. The age of the male associated with each nest, clutch-size, fledging success, and the date on which the first chick fledged were determined by regular observations of the nest. First-year males were determined to be present at a nest when two female-plumaged orioles were observed at or near the nest and both individuals were observed feeding chicks in that nest. Nestlings surviving to banding age were assumed to survive until fledging unless otherwise noted. Fledging was defined as the departure of any chick from the nest without human interference.

Results.—Thirty-four of 61 active Northern Oriole nests were accessible for data collection in 1981 and 1982. In 1981 three nests associated with first-year males had significantly smaller clutches ($t = 7.75$, df = 12, $P < 0.01$) and four nests had significantly lower fledging success ($t = 3.93$, df = 11, $P < 0.01$) than nests associated with older males. Nests with first-year males had a mean clutch-size of 2.3 ± 0.58 eggs while 5.1 ± 0.54 eggs were recorded from nests of older males. Nests with first-year males fledged a mean of 0.8 ± 0.96 chicks while 3.9 ± 1.54 chicks fledged from nests of older males.

In 1982 three nests associated with first-year males had significantly smaller clutches ($t = 5.95$, df = 12, $P < 0.01$) and four nests had significantly lower fledging success ($t = 2.17$, df = 15, $P < 0.05$) than nests associated with older males. Nests with first-year males had a mean of 3.0 ± 0.00 eggs while 4.9 ± 0.54 eggs were recorded from nests of older males. Nests with first-year males fledged a mean of 2.5 ± 1.00 chicks while 3.6 ± 0.87 chicks fledged from nests of older males.

Combining the 1981 and 1982 data, six nests associated with first-year males had significantly smaller clutches ($t = 9.51$, df = 26, $P < 0.01$) and eight nests had significantly lower fledging success ($t = 4.25$, df = 28, $P < 0.01$) than nests associated with older males. Nests with first-year males had a mean clutch-size of 2.7 ± 0.52 eggs while 5.0 ± 0.53 eggs were recorded from nests of older males. Nests with first-year males fledged a mean of 1.6 ± 1.30 chicks while 3.7 ± 1.16 chicks fledged from nests of older birds.

The period of fledging covered 19 days in 1981 and 27 days in 1982 (Fig. 1). In both 1981 and 1982 the earliest fledging from a nest associated with a first-year male was after more than half of the nests of older males had fledged (Fig. 1), indicating that nests of first-year males were initiated later than those of older males. Renesting after a nest had been destroyed was suspected twice in 1982 with nests of older males, but a second nest or second brood was not observed.

Discussion.—Johnsgard (Birds of the Great Plains: Breeding Species and their Distribution, Univ. Nebraska Press, Lincoln, Nebraska, 1979), using data on 57 oriole nests in Kansas,

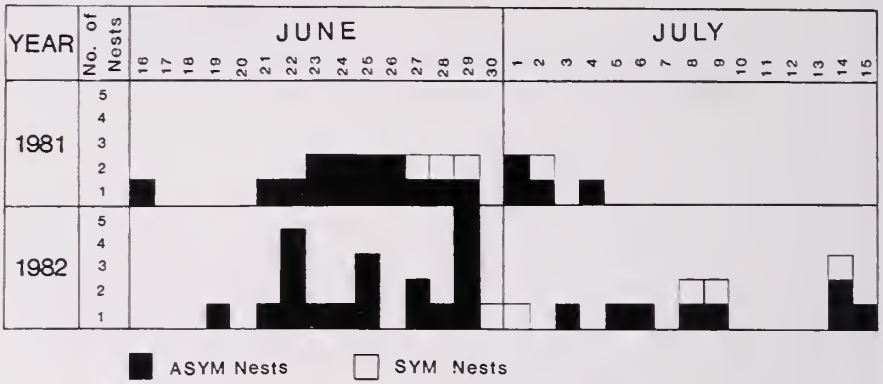

FIG. 1. Histogram of fledging dates of Northern Oriole broods near Hays, Ellis Co., Kansas, in 1981 and 1982.

and Pank (M.S. thesis, Univ. Massachusetts, Amherst, Massachusetts, 1974), studying orioles in Massachusetts, reported an average of 4.7 eggs per clutch, similar to the mean clutch-size of 4.5 ± 0.52 eggs I found when both age groups were combined. Female age appears to affect nesting productivity (Baillie and Milne, Bird Study 29:55–66, 1982); if, as has been suggested (Flood, M.S. thesis, Univ. Toronto, Toronto, Canada, 1980), orioles tend to mate with individuals of similar age (a phenomenon also reported to occur in other species [Coulson and White, Ibis 100:40–51, 1958]) this might account for the significantly smaller clutches in the nests of first-year males. It was impossible to determine the age of female orioles in this study.

The mean of 3.2 ± 1.18 fledgings per nest (when both age groups were combined) is significantly greater ($t = 5.15$, df = 67, $P < 0.01$) than the mean of 2.4 ± 1.87 calculated from data given by Pank (1974). Pank (1974) included nests with unincubated (abandoned) clutches; I had difficulty detecting such clutches (the presence of any in my sample would lower the mean number of fledglings reported herein). The significantly fewer fledgings from first-year male nests was primarily due to the significantly smaller clutches for those nests. This agrees with reports of lower fledging success for broods parented by younger birds in other species (De Steven, Ibis 120:516–523, 1978) and might suggest that younger birds are less efficient at caring for eggs and nestlings than are older nesting pairs. I visited nests too infrequently to determine whether mortality occurred in the egg or nestling stage.

Pank (1974) reported that fledging began 5 days later and lasted 4 days longer in the second season of his study, which was interrupted by inclement weather. Unpublished weather data from the Fort Hays Experiment Station, which adjoined the study area, indicate that the weather was somewhat cooler and wetter during the egg-laying period in 1982; this might have been ultimately responsible for the later (3 days) and less synchronous fledging in 1982 (Fig. 1). The late fledging of nestlings belonging to first-year males probably reflects the fact that pairs including a first-year male nested later in the season, as has been reported both for Northern Orioles elsewhere (Flood 1980) and for other species (De Steven 1978).

Lack (Population Studies of Birds, Clarendon Press, Oxford, England, 1966) and others working with other species have attributed the lowered success of younger birds at least partially to inexperience in pair bond formation, nest construction, and care of eggs and

nestlings. I have no proof that inexperience caused the lower reproductive success of first-year male Northern Orioles, but it remains a likely possibility.

Acknowledgments.—I am especially indebted to Charles A. Ely who supervised the field-work and M.S. thesis and, along with N. J. Flood, J. C. Barlow, J. D. Rising, and R. B. Payne, critically read this paper. I also thank C. Ritter, K. Navo, J. R. Choate, E. D. Fleharty, G. K. Hulett, M. E. Nelson, and the graduate students of Fort Hays State Univ. for their help during this study.—THOMAS E. LABEDZ, *Dept. Biological Sciences, Fort Hays State Univ., 600 Park St., Hays, Kansas 67601.* (Present address: *1009 West 3rd St., #3, Grand Island, Nebraska 68801.*) *Accepted 9 Dec. 1983.*

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Nesting by injured Common Eiders.—The ability to recover from broken bones and other injuries is well documented for many species of birds, particularly waterfowl (Kirby, Riechman, and Schoenfelder, Wildl. Soc. Bull. 9:150–153, 1981). Tiemeier (Auk 58:350–359, 1941) found evidence of healed bones in 4.5% of more than 6000 museum specimens examined. The highest incidence of healed injuries, 12.6%, was in the family Anatidae. The majority of those injuries were breaks in the humeri, radii or ulnae and most were judged severe enough to have prevented flight during the healing process. Similarly, Whitlock and Miller (J. Wildl. Manage. 11:279–281, 1947), after fluoroscopic examination of more than 900 ducks, found 2% had sustained wing injuries yet had recovered to fly again. Our article presents data on wild, injured ducks that did not regain the ability to fly, yet survived and appeared to behave normally in all other regards.

During nesting studies of Common Eiders (*Somateria mollissima dresseri*) on 75 coastal islands in Maine in 1981, 411 nesting females were handled. Seven had wing injuries severe enough to preclude flight. The first injured eider was found 14 May in the nesting cover of Little Birch Island, Harpswell, Cumberland Co. The distal ends of her right radius and ulna had been previously broken but were now healed, although at an angle preventing flight. On 19 May, another injured female eider was flushed from her nest and captured on Grass Ledge (West), Deer Isle, Hancock Co. The right humerus was broken and the flight feathers badly worn. She appeared healthy in all other regards.

On 3 June at Fisherman Island, Muscle Ridge, Knox Co., a female with a broken left humerus was found incubating four eggs, the average clutch-size in Maine (Choate, M.S. thesis, Univ. Maine, Orono, Maine, 1966). The wing feathers were badly worn and faded and several primaries were reduced to stubby shafts. A check of the nest on 13 June indicated a successful hatch. Also on 3 June, two nesting females, unable to fly due to wing injuries, were found on Damariscove Island, Boothbay Harbor, Lincoln Co. One was captured and had a broken left humerus and severely worn flight feathers but otherwise was in good physical condition.

On Hart Island, Port Clyde, Knox Co., a female eider with a broken left humerus was found nesting 6 June. The last injured eider was found nesting 13 June, again on Fisherman Island. Her right ulna and radius were broken. The feathers of that wing were faded and worn; several were broken. Otherwise the bird was in excellent condition, weighing 1.4 kg, which is near the Maine average at the mid-point of incubation (Korschgen, J. Wildl. Manage. 41:360–373, 1977). A subsequent nest inspection proved a successful hatch.

The extent of bone healing, the degree of feather wear, the retention of feathers on at least three injured wings through the previous annual molt, and the similarity of these injuries to wounds expected from the hunting season indicated all seven birds had been unable to

fly since well before nesting. For at least three, the injuries were old enough to have prevented migration that spring and probably the previous autumn. From the standpoint of avian physiology and behavior, it is noteworthy that the injured eiders fed, courted, nested, and survived without the ability to fly or migrate.

While feeding, the wings aid in diving but are not used while on the bottom (Palmer, Handbook of North American Birds, Vol. 3:49, Yale Univ. Press, New Haven, Connecticut, 1975). Foraging efficiency could then be reduced in crippled birds. However, the eiders we encountered had been able to deposit the large fat and protein stores needed for egg production and as an energy source throughout incubation (Korschgen 1977). During courtship the female has a rather passive role (Palmer 1975), thus, the loss of flight should not hinder pairing and mating. The inability to migrate would likely be little problem to Maine eiders, since suitable feeding areas, for all seasons, occur nearby the nesting islands. Furthermore, banding analysis of *S. m. dresseri* (Wakely, M.S. thesis, Univ. Maine, Orono, Maine, 1973) suggests a portion of Maine's breeding eider population is essentially non-migratory.

Our 1981 observations then indicate that eiders in Maine may be better adapted than other North American waterfowl to function in the wild, in a nearly normal manner, in spite of sustaining flight-impairing injuries. The many similarities between the eider and the two flightless species of South American Steamer Ducks (*Tachyeres pteneres* and *T. brachypterus*) add strength to this conclusion.

Possible sources of these injuries include gunshot wounds, encounters with predators, battering against ledges during severe storms, or collisions with branches or ledges while landing on or leaving nesting islands. During the handling of several thousand nesting eiders in Maine since 1964 injuries have been observed, although infrequently (Mendall and Hutchinson, unpubl.). For example, on Fisherman Island, of 833 nesting birds caught prior to 1981, only two had injuries precluding flight. We have no explanation, other than normal, random variation, as to why more injured birds were found in 1981.

We extend our thanks to Betty Jackson, Maine Department of Inland Fisheries and Wildlife for her skill in editing and typing this manuscript.—Howard L. Mendall, *P.O. Box 133, Brewer, Maine 04412;* Alan E. Hutchinson, *Maine Dept. Inland Fisheries and Wildlife, P.O. Box 1298, Bangor, Maine 04401;* and Ray B. Owen, *College of Forest Resources, Nutting Hall, Univ. Maine, Orono, Maine 04469.* *Accepted 3 Feb. 1984.*

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Distribution and phenology of nesting Forster's Terns in eastern Lake Huron and Lake St. Clair.—Forster's Terns (*Sterna forsteri*) are considered to be a prairie, East Coast (Erwin, Coastal Waterbird Colonies: Cape Elizabeth, Maine to Virginia, FWS/OBS–79/10, 1979) and Gulf Coast (Portnoy, Proc. Colonial Waterbird Group 1:38–43, 1977) nesting species. A concentration of more than 200 nests has been known from four sites in Lake Michigan near Brown and Oconto Counties, Green Bay, Wisconsin (Scharf et al., Nesting and Migration Areas of Birds of the U.S. Great Lakes, Fish and Wildlife Service, OBS–77/2, 1979). Kenaga (Jack-Pine Warbler 35:68–70, 1957) found at least two pairs of nesting Forster's Terns in the Saginaw Bay area of Michigan in 1956 and historically the species was considered to breed commonly at Lake St. Clair (Morden and Saunders, Canadian Sportsman and Naturalist, 1882:194). Several other accounts are given from the late 1800 to early 1900 period by Campbell and Trautman (Auk 53:213–214, 1936). Sightings of up to 25 nesting pairs of Forster's Terns have been noted on the Canadian portion of Lake St. Clair (James et al., An Annotated Checklist of the Birds of Ontario, Life Sci. Misc. Publ., Royal Ont.

TABLE 1
LOCATION AND NUMBER OF FORSTER'S TERN COLONIES 1980 AND 1982

	Colony name	Area	Lat., long.	No. nests 1980	No. nests 1982
1.[a]	East Standish	Northern Saginaw Bay	43°58′N, 084°10′W	10	6
2.	Channel-Shelter Dike	Middle Saginaw Bay	43°40′N, 084°15′W	50	145
3.	Sebewaing	Southeastern Saginaw Bay	43°45′N, 083°35′W	0	240
4.	Clinton River S	Northern Lake St. Clair	42°34′N, 082°41′W	29	80
5.	Clinton River N	Northwestern Lake St. Clair	42°34′N, 082°41′W	4	50
6.	Baltimore Hwy. 1	Northwestern Lake St. Clair	42°36′N, 082°39′W	0	20
7.	Baltimore Hwy. 2	Northwestern Lake St. Clair	42°36′N, 082°39′W	0	50
8.	Baltimore Hwy. 3	Northwestern Lake St. Clair	42°36′N, 082°39′W	0	16
9.	Cresent	Northwestern Lake St. Clair	42°38′N, 082°39′W	0	210
10.	Round	Northwestern Lake St. Clair	42°39′N, 082°38′W	0	33
11.	L-shaped	Middle Lake St. Clair	42°37′N, 082°44′W	7	0
	Total			100	850

[a] Numbers indicate locations of colonies on Fig. 1.

Mus., Toronto, Canada, 1976; Goodwin, Am. Birds 30:950, 1976; 31:1131–1135, 1977; 32:1154, 1978; 33:858–860, 1979; 35:935, 1981). Nesting of 12–50 pairs is also recorded in Ontario at Long Point (Goodwin, Am. Birds 30:950, 1976) and at Point Pelee (Goodwin 1977). However, Campbell (Birds of the Toledo Area, The Blade, Toledo, Ohio, 1968) notes that no evidence of breeding has been found in the nearby and apparently suitable habitat of western Lake Erie. This also agrees with our surveys of the Lake Erie area (Scharf, Colonial Birds Nesting on Man-Made and Natural Sites in the U.S. Great Lakes, Tech. Rept. D–78–10 Waterways Exper. Stat., Vicksburg, Mississippi, 1978; Scharf et al. 1979; Shugart and Scharf, J. Field Orn. 54:160–169, 1983). In this note, we describe increasing numbers and colonies of nesting Forster's Terns in eastern Lake Huron's Saginaw Bay and Lake St. Clair, habitat preferences, and nesting cycle.

Methods.—Forster's Tern colonies were located from a Cessna 180 floatplane at an altitude of 100–150 m above lake level during May, June, and July of 1980 and 1982. We searched the entire Michigan Great Lakes in 1980, and in 1982 searched the area designated Ludwig Survey Area by Shugart and Scharf (1983) in conjunction with a survey of breeding Common Terns (*S. hirundo*). Upon locating a colony we landed and waded in mud and water up to

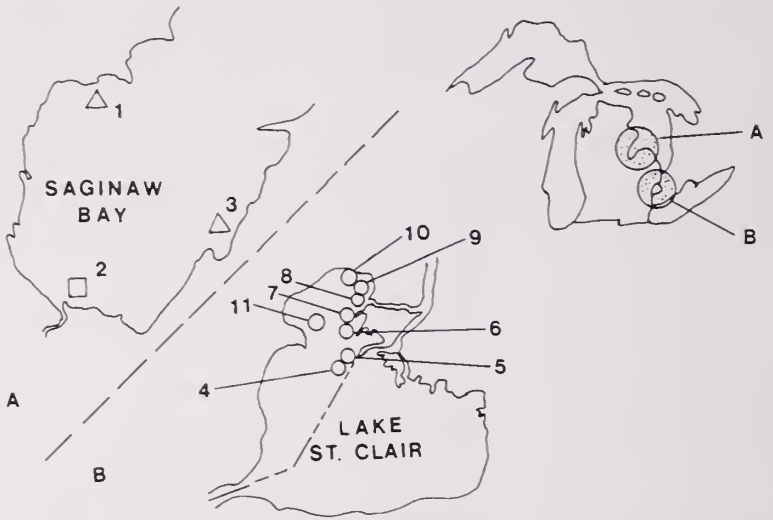

FIG. 1. Map of Forster's Tern colony sites. Numbers correspond to Table 1. Circles are colonies in *Phragmites*, triangles are colonies in *Typha*, and the square represents dredged disposal covered with *Polygonum*.

1.3 m deep to make most nest counts. The Channel-Shelter Diked Disposal (CSDD) was an exception where we walked over quaking dredged material to the nests. A few nest counts represent aerial counts of sitting (i.e., incubating) terns.

Vegetation type (reedgrass [*Phragmites communis*], cattail [*Typha* sp.]) was identified during visits to colonies. We recorded colony-sites on 1:40,000 scale navigation maps, photographed sites, nests and young, and banded young where possible.

Results.—We located five colonies and 100 nests in 1980, and 10 colonies and 850 nests in 1982 (Table 1). All colonies were in marsh habitat in Saginaw Bay and Lake St. Clair (Fig. 1). Only one of the 1980 sites was unused in 1982; the remainder had increased in numbers of pairs in the interim. Since the same area was searched in both years, the totals represent a substantial increase in the number of colonies and nesting pairs for this area.

The Forster's Tern colonies we located were in three distinct habitats: (1) cattail and mud islands; (2) reedgrass islands which were rooted in water and mud up to 1.5 m deep; and (3) near the standing water-emergent smartweed (*Polygonum* sp.) interface in the interior of a partially filled dredge-material disposal and containment site (CSDD).

At the cattail and mud islands nests were placed in floating broken stems of vegetation, bare mud, and on muskrat (*Ondatra zibethica*) houses. The *Phragmites* island sites were most common (7/10 sites) in 1982. In these, nests were placed on floating mats of dead vegetation, primarily *Phragmites*, and flotsam which had accumulated around an erect central core of the previous year's growth. These mats apparently were formed by ice and wave action. The mats and the birds were not visible from water level because of a concentric zone of new growth on the outside of the mats. A similar zonation of nests was evident in the *Polygonum*-water interface at CSDD. At this site water receded, leaving the once floating nests on mud.

Common Terns nested within 100 m of the Forster's Terns at two sites (CCDS, Clinton

River) on drier and less vegetated substrate. We saw no Black Terns (*Chlidonias niger*) near the Forster's Tern sites in contrast to Bergman et al. (Wilson Bull. 82:435–444, 1970). Only two Forster's Tern nests were placed on muskrat houses, although muskrats and their houses were common. This infrequent use of muskrat houses contrasts with 53–98% of the nests on muskrat houses in Iowa (Bergman et al. 1970; Weller and Spatcher, Spec. Rept. 43, Iowa St. Univ., Ames, Iowa, 1965). From the third week of May to the first week of June 1982, 67% of nests at which clutch-size was recorded, had three eggs. In 1980, sites checked in the first 2 weeks of June had nests under construction and incomplete clutches which suggests a prolonged nesting cycle or renesting. These observations of nesting chronology are consistent with the Iowa data of Bergman et al. (1970).

Discussion.—Based on published information, Forster's Terns, during most of this century, were uncommon and scattered nesters in southern Lake Huron and Lake St. Clair, and the lower Great Lakes. This is no longer true. This species must be considered common in our survey area. The increase we describe represents a substantial shift from the discontinuous breeding range usually described for this species, and shows a concentration of breeding colonies from southeastern Michigan through southwestern Ontario. Perhaps the recent increase represents a return to former numbers and distribution. Or, the rapid increase may be a response to greater food and nesting site availability coupled with the loss of competition from a closely related species, the Common Tern. The latter species has recently lost habitat (Shugart and Scharf 1983) due to high water levels. Forster's Terns, in this study area, are less vulnerable to flooding with their floating nests, and seem to have a longer period of nest initiation than Common Terns.

We assume that such a large increase in such a short time of 1976–77 to 1982 signals an ecological change of unknown magnitude. At this time we have no basis for further speculation.

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Post-fledging departure from colonies by juvenile Least Terns in Texas: implications for estimating production.—Least Terns (*Sterna antillarum*) have been classified as endangered in California since 1973 (Bureau of Sport Fisheries and Wildlife, Resour. Publ. No. 114, 1973), and decline in numbers has been suggested for much of its range in North America and for the similar Little Tern (*Sterna albifrons*) in Europe (Nisbet, Bird-Banding 44:27–55, 1973; Fisk, Am. Birds 29:15–16, 1975; Lloyd et al., Br. Birds 68:221–237, 1975; Arbib, Am. Birds 33:830–835, 1979; Tate and Tate, Am. Birds 36:126–135, 1982). Despite a generally accepted decline, quantitative evaluations of reproductive parameters are few, aside from estimates of fledging success or fledgling : adult ratios presented by Massey (Proc. Linnaean Soc. N. Y. No. 72:1–24, 1974), Blus and Prouty (Wilson Bull. 91:62–71, 1979), and Massey and Atwood (Auk 98:596–605, 1981).

Earlier reports on Least Tern breeding biology often referred to counts of juveniles at colonies as a direct measure of annual productivity, and these counts were acknowledged as the usual method to estimate survival to fledging (Massey 1974). Massey and Atwood

(1981) recently suggested that more intensive work at colonies provides better estimates. The general body of Least Tern literature, however, still implies that counts of fledglings can provide a direct estimate of annual production. In this paper, we examine colony tenure by recently fledged Least Terns with regard to potential bias in the assessment of production based on juvenile counts at colonies. Further, we discuss how such counts might be improved if used in lieu of more intensive studies.

Methods.—Data were collected during the 1979 and 1980 breeding seasons at four colonies in Aransas and San Patricio counties on the central Texas coast: (1) Aransas Pass is a mainland site on a dredged material disposal area created early in 1979; (2) Copano Shell Island is a 0.05-ha natural shell island about 40 m from the mainland in a secondary bay system; (3) Portland (Sunset Lake) is a 2.3-ha sand and shell area between a tidally influenced lagoon and a heavily traveled highway; and (4) Rockport (Little Bay) colony is at a public beach and park and has existed for at least 25 years despite routine human disturbance. The flora at all sites is characteristic of species found on natural and disturbed saline substrates as described by Jones (Flora of the Texas Coastal Bend, Mission Press, Corpus Christi, Texas, 1977:xix) and Lonard and Judd (Southwest. Nat. 25:313–322, 1980).

Juvenile terns 12 days of age or older were captured by hand at colonies from late May to late July during each year. Individually identifiable Herculite® or Saflag® tags were attached to each wing with a stainless steel clip that pierced the patagium. Tags and clips approximated 2.5% of fledging weight. Fledging dates for each juvenile were estimated based on developmental stages described by Jackson (Miss. Kite 6:25–35, 1976) and judged to be accurate within 2 days based on known-age chicks. Fledging was considered to be the age at first flight as discussed by Burger (pp. 367–447 *in* Behavior of Marine Animals, Vol. 4, J. Burger, B. Olla, and H. E. Winn, eds., Plenum Press, New York, New York, 1980).

Colonies were visited approximately weekly to locate marked juveniles from first fledging during the last week of May through August each year. During each visit, the colony proper and loafing areas were examined one to five times with 7× binoculars and 20× spotting scope. Thorough visual examination of use-areas for marked terns was conducted at distances of 20–100 m, depending on tern tolerance, prior to causing any upflight. Duration of our presence near colonies was 20–500 min depending on the colony nesting population and other work in progress. The average visit was 138.5 ($N = 23$) and 146.1 ($N = 28$) min in 1979 and 1980, respectively, during which terns were disturbed only periodically. Visits were made during all daylight hours from 06:00–23:00 CDT; 20% of visits included periods between 18:00 and darkness.

A probability value was assigned to the detection of marked juveniles using a colony site during any visit. In estimating this probability, each juvenile was assumed to be using a colony from the fledging date until the last visit observed. The number of visits seen divided by the potential visits present was used as a measure of detection for each individual. The average of all observations represented the generalized detection probability.

Results and discussion.—Tags were applied to 93 juvenile terns, of which a minimum of 59 (63.4%) were known to have fledged eventually. Only 20 tagged young were known or suspected to have died prior to fledging. Thus, as many as 73 (78.5%) may have survived to fledging, a rate that is comparable to the 76.8 ± 2.0% (2 SE) fledging rate estimated independently for banded young (unpubl.).

Observations during at least four weekly visits post-fledging yielded estimates of duration of presence at colonies for 58 tagged juveniles. Twenty-six of these juveniles (44.9%) were not seen at colonies more than 2 weeks post-fledging and 86.3% were not seen after 3 weeks (Table 1). There was no significant trend in departure times between the first one-half of juveniles that were marked each year and those that were marked and fledged later in the fledging period (Cox-Stuart test, $P > 0.25$, Daniel [Applied Nonparametric Statistics, Hough-

TABLE 1
DURATION OF COLONY TENURE BY MARKED LEAST TERN JUVENILES ON THE TEXAS GULF COAST, 1979–1980

Days after fledging	Terns departing in time interval					
	1979[a]		1980[a]		Combined	
	N	%	N	%	N	%
0–7	5	16.7	2	7.1	7	12.1
8–14	7	23.3	12	42.9	19	32.8
15–21	13	43.3	11	39.3	24	41.4
22–28	2	6.7	3	10.7	5	8.6
>28	3	10.0	0	0	3	5.1
Total	30		28		58	

[a] Departure interval frequencies did not differ between years ($\chi^2 = 5.91$, df = 4, $P > 0.20$).

ton-Mifflin Co., Boston, Massachusetts, 1978:58]). Further, there was no monotonic relationship between fledging date and departure interval for all tagged young (Spearman $r = -0.082$, df = 57, $P > 0.10$). Therefore, the tabulated departure schedule was consistent from early June through mid-August. It is possible that extremely late-fledged young (> 15 August) could exhibit shorter departure intervals as colonies become deserted toward the end of the breeding season, but that time period was not represented in this data set and generally would comprise a minor component of total young fledged. None of the three juveniles shown as departing at >4 weeks was seen anytime prior to their last known presence at colonies; they likely left colonies very early and then revisited much later. Detection probability was similar both years, averaging 0.67 ± 0.02 (SE) overall.

Several potential explanations exist for the distribution of departure intervals. First, excessive mortality among marked chicks during the first 3 weeks post-fledging would yield similar data. However, 12 of the 58 juveniles (20.7%) included in this analysis were subsequently seen away from their natal colony from 10–44 days post-fledging. Thus, the 86% disappearance rate by week 3 (Table 1) exceeded the maximum possible mortality rate. Two juveniles tagged at other less intensively studied colonies were seen more than 6 weeks post-fledging at 90–200 km away from original colonies.

Second, older marked juveniles may have been using colonies but were not seen or were away at the time of visits. These explanations are possible, but the detection probability approached 70% and marked individuals known to be present generally were seen regardless of time of visit. Our observations did not discount juveniles using colonies only as nighttime roosts, but visits near dusk did not indicate that previously unseen juveniles were present then. Nighttime roosting areas used by recent fledglings may be far removed from the colony of origin (Massey and Atwood 1981).

The final possibility is that juveniles departed the colonies soon after fledging. This explanation seems most acceptable considering: (1) the probability of detecting fledglings using a colony; (2) the consistent observations within and among years of the study; and (3) the resightings of marked juveniles away from colonies. This conclusion is further substantiated by similar departure times in other areas. Juvenile Least Terns in California were seen away from natal colonies from 16–28 days post-fledging (Massey 1974, Massey and Atwood 1981). Band recovery data through August 1980 contain records of eight juveniles from the eastern

TABLE 2

COMPARISONS AMONG ESTIMATES OF FLEDGLING PRODUCTION AT THREE TEXAS COASTAL LEAST TERN COLONIES, 1979–1980

Colony	Year	Est. breeding pairs	Est. total fledged[a]	Single highest fledgling count	Sum of fledgling counts relative to breeding chronology[b]		Est. total fledglings corrected for early departure[c]
					Within colony chronology	Inter-colony chronology	
Rockport	1979	112	90–100	45	98	83	104
Rockport	1980	140	110–120	47	94	63	100
Aransas Pass	1980	88	35–40	15	17	20	24
Copano Shell Is.	1980	26	15–18	7	7	4	8

[a] Estimates based on reproduction studies conducted concurrently.

[b] Estimates = sum of counts made at peak fledging, 4 weeks, and 8 weeks after peak fledging.

[c] Estimate = [$\text{Count}_{(1)}$ made during second week of fledging coastwide] plus [$\text{Count}_{(2)} - 0.55(\text{Count}_{(1)})$] plus $\sum_{i=3}^{n} [\text{Count}_{(i)} - 0.05(\text{Count}_{(i-2)}) - 0.55(\text{Count}_{(i-1)})]$. Where i = the numerical sequence value of counts at 2-week intervals and n = the total number of counts.

U.S. that were found outside the 10-min block where banded from 3–22 days after banding and thus <3 weeks post-fledging. While this evidence of rapid departure has been available for some time, implications toward estimation of annual production apparently was not previously recognized, at least not in published form.

The fledging chronology observed in the Texas colonies involved in this study spanned 12 weeks, with 8 weeks required for completion of 90% of the fledging during both years. Contrasting these time periods with the brief colony tenure of marked juveniles reveals a potential bias in the relationship between juvenile counts and cumulative survival to fledging. Counts of fledglings at colonies likely represent only the young fledged during the previous 2–3 weeks. Such counts would substantially underestimate total success and would be difficult to interpret unless conducted at similar breeding stages in each colony and often enough to include most young prior to their departure.

Limited data collected at three colonies during 1979–1980 verified that single counts of juveniles substantially underestimated total production (Table 2). In contrast, multiple counts timed with the breeding chronology (especially those corrected for fledgling departure) provided more realistic estimates of survival to fledging. With adequate information concerning regional breeding chronology, the potential exists for using multiple counts of juveniles to assess annual production of Least Terns throughout their range. A suitable correction was obtained for the Texas colonies studied by using five–six counts starting 2 weeks into fledging and continuing at 2-week intervals until fledging was complete. The formula for this departure correction is footnoted in Table 2. The multipliers in this formula (0.55 and 0.05) represent the proportion of previously counted fledged juveniles expected to be present during repeated visits to colonies based on data in Table 1. Observer familiarity with temporal and spatial aspects of each colony should dictate proper timing of counts and area examined.

The data presented here apply to Texas and are necessarily preliminary; empirical verification in other areas is warranted. These procedures provide a means of estimating production when only brief visits to colonies at lengthy intervals are possible and the intent is

to obtain gross estimates over large areas. Consideration should be given to evaluating applicability to other precocial colonial ground-nesting species whose fledgling survival may be inaccurately estimated by "traditional" counts. Procedures may be especially applicable during future fieldwork designed to compile geographic summaries of waterbird nesting status like those of Erwin (Coastal Waterbird Colonies: Cape Elizabeth, Maine to Virginia, U.S. Fish and Wildl. Serv., FWS/OBS–79/10, 1979) and Sowls et al. (Catalog of California Seabird Colonies, U.S. Fish and Wildl. Serv., FWS/OBS–80/37, 1980). These procedures are not suggested for colonies where ongoing studies can provide more detailed data for production estimates and associated confidence limits.

In summary, the majority of juvenile Least Terns appear to depart colonies within 3 weeks after fledging. Single counts of fledged juveniles substantially underestimate cumulative production. Awareness of these phenomena will permit more accurate assessment of fledging rate for Least Terns. At a minimum, multiple counts should be made on a schedule timed with the breeding chronology in the survey area and should be corrected for juvenile departure. Observer familiarity with colonies is requisite to the appropriate timing of counts and examination of use areas. Counts using such procedures are not suggested as substitutes for estimates derived from more intensive studies of survival.

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Expanded use of the variable circular-plot census method.—Since its introduction by Reynolds et al. (Condor 82:309–313, 1980), the variable circular-plot method (VCPM) has become a popular means of censusing birds (Ralph and Scott, eds., Stud. Avian Biol. 6, 1981). Designed for use in rough terrain, the method has now been applied in a variety of vegetation types (e.g., DeSante, Stud. Avian Biol. 6:177–185, 1981; Morrison et al., Stud. Avian Biol. 6:405–408, 1981; Scott et al., Wildl. Soc. Bull. 9:190–200, 1981a). The method allows density estimates based on species-specific detection distances obtained by observers at fixed locations. The method assumes, however, that individual birds are located anywhere within the species-specific radius around the fixed point; that is, locations of individuals are not mapped as with the classic spot-map method (SMM; Williams, Ecol. Monogr. 6:317–408, 1936; Kendeigh, Ecol. Monogr. 14:67–106, 1944; see also Ralph and Scott 1981). The SMM provides an estimate of territorial bird density and is often used for assessing the accuracy of other methods (Franzreb, Stud. Avian Biol. 6:164–169, 1981; Szaro and Jakle, Wilson Bull. 94:546–550, 1982). The SMM, however, is usually applicable only to small areas of moderate terrain during the breeding season (Emlen, Auk 94:455–468, 1977). This paper describes a simple way to use the VCPM as a means of: (1) locating areas of highest use by birds, (2) rudimentarily delineating territories, and (3) assessing the problems of double-counting individuals.

The method.—The only information required in addition to that recorded for standard VCPM counts (Reynolds et al. 1980) is the direction of the bird from the census station. A compass can be hand-held or attached to a clipboard and the direction (azimuth) of each individual bird seen or heard can be recorded along with distance and other information of

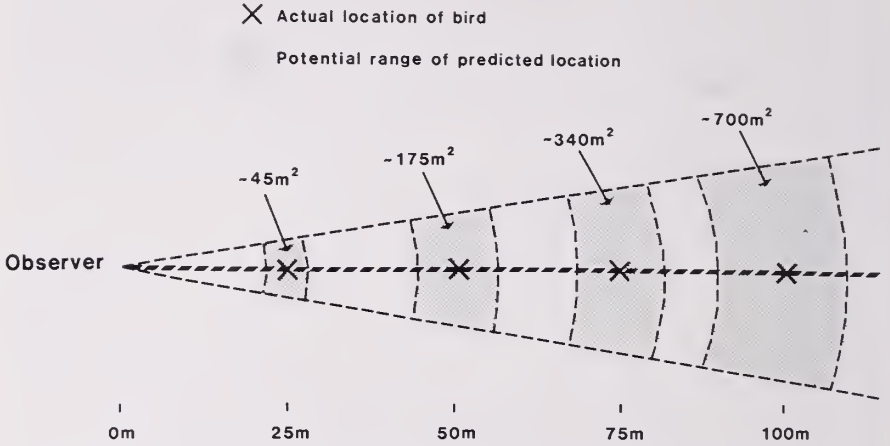

FIG. 1. Potential ranges of predicted locations of birds at four distances from observer, assuming 10% error in both direction and location.

interest. As direction is not required for calculating estimates of bird densities with the VCPM, missing data on directions would not affect density estimates. Direction and distance data can then be used to estimate the positions of the birds.

Given repeated censuses, territories may be roughly located as in the SMM using maps of the study area; sample sizes required for estimating density by the VCPM and SMM were described elsewhere (Robbins, Audubon Field-Notes 24:723–726, 1970; Reynolds et al. 1980; Franzreb 1981, Morrison et al. 1981). The use of direction estimates in the VCPM is offered not as a means of determining true territory boundaries and territory size, but rather for identifying areas of higher activity through a concentration of observations as plotted on maps. Birds could thus be located on a study area of any size without establishing a grid system, and densities could be calculated. With adequate numbers of observations of territorial species, density estimates derived from the VCPM could be compared with those obtained from mapping. Possible overlap (double-counting) of birds between adjacent stations could also be evaluated by mapping. Double-counting of individuals is a major problem with the VCPM (Reynolds et al. 1980) but has not been critically evaluated. Some of the problems of delineating territories using a mapping scheme were reviewed by Eagles (Stud. Avian Biol. 6:455–460, 1981), Franzreb (1981), and Oelke (Stud. Avian Biol. 6:114–118, 1981). Combining the recording of distance and direction would also allow calculation of densities on a year-round basis; densities of non-breeding species usually cannot be calculated using the SMM alone (Franzreb 1981).

Considerations of bias.—Incorporating direction into the VCPM requires an accurate estimation of both distance and direction. Errors in estimating these parameters increase with increasing distance from the census point. Methods of training observers to use the VCPM should be considered (e.g., Kepler and Scott, Stud. Avian Biol. 6:366–371, 1981; Scott et al., Stud. Avian Biol. 6:334–340, 1981b).

Scott et al. (1981b) noted that mean estimates of distances to birds heard were accurate within 10%, although the variance of distance estimates made by any one observer may be quite high. Our experience suggests that 10% is also a reasonable estimate of mean observer

error in determination of direction (unpubl.). Of course, the exact level of error may vary among observers, habitats, and with absolute distance of an observation. Assuming 10% error, errors in distance and direction estimation thus may be viewed as frustrums of wedges that increase in area with increasing distance from the observer (Fig. 1). Accurate estimation of direction and distance may be difficult in extremely rough terrain, where across-ground direction and distance estimates are desirable. In such cases, however, mapping locations will still indicate general areas of higher use by birds.

Extensive evaluation followed the formal introduction of the VCPM (such as in Ralph and Scott 1981). The use of direction estimates to delineate territories must also be evaluated. We are using the addition of directional data to the VCPM to help assess habitat use; these results will be presented elsewhere.

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Evaluation of the road survey technique in determining flight activity of Red-tailed Hawks.—Road censusing, as described by Craighead and Craighead (Hawks, Owls and Wildlife, Stackpole Co., Harrisburg, Pennsylvania, 1956), has been used extensively in Christmas bird counts to assess raptor population densities. Observations of activity of raptors during such surveys have been used to indicate the overall activity pattern of a species (Craighead and Craighead 1956; Schnell, Auk 84:173–182, 1967; Bildstein, Ph.D. diss., Ohio State Univ., Columbus, Ohio, 1978; Preston, Wilson Bull. 93:350–356, 1981). However, there are no studies that verify that road censusing techniques provide an accurate estimate of the flight activity pattern of raptors. In this report I assess the applicability of the road survey technique for determining the amount of daily flight of the Red-tailed Hawk (*Buteo jamaicensis*) by comparing this method with results obtained from direct long-term observations of individuals. Red-tailed Hawks are good candidates for the census technique (Fuller and Mosher, Stud. Avian Biol. 6:235–248, 1981), since they tend to use open habitat and frequently hunt along roadsides.

In order to obtain an accurate estimate of the actual percentage of the day spent in flight, a bird must be equally visible during all activities. As raptors often change their activity patterns at certain periods of the day, it is also essential that all periods are equally represented in the sample. Seasonal changes in activity patterns and behavior of certain individuals occurring, for example, during breeding, migration, or fledging, should also be taken into account.

Methods.—Road surveys of Red-tailed Hawks were made during winter (5 December 1981–28 February 1982) and during summer (23 June–16 September 1982). Over 4000 km were driven (32–72 kmph [20–45 mph]) each season along roadway transect routes in central Missouri (38°49′N lat.). These intervals were chosen to minimize the possibility of observations of breeding or migratory hawks, but still at such times to enable me to compare activity patterns typical of summer and winter. Routes were travelled repeatedly, but only once per field day, by one to three observers. When a bird was first observed, the time of day and activity (either flying or perched) was recorded. The vehicle was stopped momentarily if a bird could not be identified. Only birds within approx. 0.4 km of either side of a road were included. When driving unfamiliar transects and/or ones along which topography

TABLE 1

ACTIVITY OF RED-TAILED HAWKS THROUGHOUT THE DAY AS DETERMINED BY THE ROAD SURVEY TECHNIQUE

Time period	Summer		Winter	
	Total seen	% perched	Total seen	% perched
06:00–09:00[a]	46	95.6	113	87.6
09:00–12:00	47	89.4	110	84.0
12:00–15:00	28	75.0	50	90.0
15:00–18:00	34	97.1	77	88.3
18:00–21:00	6	100.0	—	—
Total	161	90.7	340	87.1

[a] Times are DST for summer and CST for winter.

or vegetation (particularly in summer) made birds more difficult to detect, the driving speed was reduced and the number of observers increased.

To evaluate the road census technique, individual Red-tailed Hawks were watched for intervals longer than any bird was observed during a transect run. This lengthy observation, done with a 40× telescope, occurred concurrently with transect runs. I conducted 107 observation sessions totalling 113.5 h from 13 December 1981–24 February 1982, and 96 observation sessions totalling 122.7 h from 8 July–14 September 1982. Birds were not marked, therefore the total number of individuals included in the sample is not known, but observation periods often involved what seemed (by behavior, location, and/or plumage) to be the same bird. Activity of a bird was monitored continuously during an observation session. The percentage of time a bird perched at heights above 6.0 m and on the ground were noted during time budget observations.

Results.—As determined by the road survey technique, birds flew 9.3% of the daylight hours in summer and 12.9% of the time in winter. These estimates are nearly twice those

TABLE 2

ACTIVITY OF RED-TAILED HAWKS THROUGHOUT THE DAY AS DETERMINED BY LONG-TERM OBSERVATION

Time period	Summer		Winter	
	Total obs. time (sec)	% perched	Total obs. time (sec)	% perched
06:00–09:00[a]	86,783	97.6	68,986	95.5
09:00–12:00	93,171	92.6	126,809	94.2
12:00–15:00	84,536	89.2	122,686	90.4
15:00–18:00	104,868	97.1	89,972	93.6
18:00–21:00	72,323	98.8	—	—
Total	441,681	95.0	408,453	93.2

[a] Times are DST for summer and CST for winter.

TABLE 3

CHI-SQUARE TESTS FOR GOODNESS-OF-FIT OF DAILY ACTIVITY AS DETERMINED BY ROAD SURVEY DATA COMPARED TO THAT DETERMINED BY LONG-TERM OBSERVATION

Time period	Summer		Winter	
	χ^2	P[b]	χ^2	P
06:00–09:00[a]	0.15	NS	14.58	0.005
09:00–12:00	0.32	NS	17.22	0.005
12:00–15:00	4.48	0.05	0.04	NS
15:00–18:00	0.25	NS	2.77	NS
18:00–21:00	0.47	NS	—	—

[a] Times are DST for summer and CST for winter.
[b] df = 1 in all tests.

measured by long-term visual observations of individual birds (5.0% and 6.8% for summer and winter, respectively; Tables 1, 2). Using the latter data as the expected proportion of flight and perching in a standard Chi-square test, there were no significant differences between road surveys and long-term observation data for different times of the day (Table 3) except during the summer afternoons, and winter early morning and late morning. Lumping all observations regardless of time, the null hypothesis was rejected for summer ($P \leq 0.025$) and for winter ($P < 0.005$).

During long-term observations in summer, perched hawks were on the ground 1% of total perched time and higher than 6.0 m, 8.4% of the time. However, during winter, perched hawks spent 3% of their total perched time on the ground and 35.1% of the time on perches higher than 6.0 m. These seasonal differences in perch height may have influenced the visibility of perched hawks during road surveys.

Discussion.—The over-estimate of flight time using the road census technique probably results from an under-representation of the number of perched birds observed during the census. Although hawks typically used high perches in summer and were seldom on the ground, perched birds were often difficult to detect after foliage growth. Morning and evening times during summer showed close agreement between the census technique and the time budget. I found the largest difference between the two techniques for the afternoon period—25.0% flight time as assessed by surveys compared to 10.8% observed in the time budget. During summer afternoons, hawks soared for long periods. Compared to perched or low flying hawks, a soaring bird is much more obvious, particularly at great distances. This increased detectability may have biased the census, resulting in an inaccurate measure of flight activity.

I expected the census data to provide a more accurate estimate of flight activity in winter than summer, because the leafless condition of deciduous trees would make perched birds more visible. However, the winter road survey total for flight was almost twice as high as that observed during the time budget. Perhaps perched Red-tailed Hawks were difficult to detect because they used lower perches in winter. Hawks spent 64.9% of their perched time at heights below 6 m, where they were extremely difficult to detect on road surveys. In many cases hawks used fence posts 2 m high and thus may have been hidden in depressions or behind brush during a road census.

The winter census agreed with the time budget for the afternoon and evening periods, while the morning time periods over-estimated flight time. Assuming low perch height was

responsible for under-representation of perched hawks during morning periods, why was the afternoon road census estimate more accurate? By mid-day hawks are no longer hunting intensely and have moved up to higher perches, where they can maximize radiant absorption as well as competitor detection and territory defense. Observation of perched hawks during a census would be enhanced during these periods thus providing more accurate estimates of activity.

Although the road survey technique is not always accurate for the Red-tailed Hawk, this does not mean that the technique is an imprecise estimator of activity patterns for other species. Activity of Rough-legged Hawks (*B. lagopus*) may be more accurately gauged by the survey technique, since they tend to hunt in more open habitat (Weller, Iowa Bird Life 34:58–62, 1964) making perched birds more obvious. Schnell (1967) in fact used the road census technique to assess the influence of various environmental factors on flight of this species. Activity of larger raptors such as eagles (e.g., Golden Eagle [*Aquila chrysaetos*]), may be more accurately estimated by the road census technique because their larger silhouette is more conspicuous, while the converse may be true for smaller birds of prey (e.g., American Kestrels [*Falco sparverius*]). On the other hand, the road census may be an entirely invalid estimator of activity of some species due to their specific behavioral patterns. For example, Northern Harriers (*Circus cyaneus*) fly a large percentage of the day, but much of their perched time is spent on the ground (Weller, Wilson Bull. 67:189–193, 1955) where they are not always visible. Therefore, before using a survey method for determining activity patterns of raptor species, workers should consider factors I have noted above which affect detectability of perched birds (especially perch-site selection).

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Extreme aggression in Great Blue Herons.—Meyerriecks (Publ. Nuttal. Ornith. Club 2: 98, 1960) noted that contact during aggressive interactions between Great Blue Herons (*Ardea herodias*) was quite rare and he never observed a fight which resulted in damage to either of the combatants. Benson and Penny though (Philosophical Trans. Royal Soc. Lond. B. 260:417–527, 1971) reported an immature Grey Heron (*A. cinerea*) was stunned fighting with another Grey Heron, and Woolfenden et al. (Bird-Banding 47:48–53, 1976) reported starving Cattle Egrets (*Bubulcus ibis*) occasionally grabbed at one another with their toes and pecked during brief fights. The present note describes two observed and one apparent case of extreme aggression by Great Blue Herons.

On 18 July 1982 at 18:00 near the Creston Valley Wildlife Interpretation Centre (CVWIC) at Creston, British Columbia, a young-of-the-year heron carrying a black bullhead (*Ictalurus melas*) landed about 100 m away from a foraging adult heron in an area where earlier an adult heron defended a territory about 300 m in radius. After 30 sec the juvenile, still carrying the bullhead, flew to a location about 20 m from the adult and assumed an aggressive upright display, followed by a forward display (see Meyerriecks 1960). The adult then flew at the juvenile, and landed on its back. The two herons stabbed with their bills and buffetted each other with their wings for about 20 sec before the adult, using its feet, gripped the juvenile's neck and submerged its head and body. About 20–30 sec later the juvenile heron lifted its head above water, still holding the bullhead. The adult struck its bill toward the

juvenile's head but missed. The juvenile swallowed the bullhead and began sparring with the adult while vocalizing between strikes. Once, the adult's bill struck down to the back of the throat of the juvenile, which caused an injury. After that the herons were startled by a shout and the adult flew and landed about 300 m away, the juvenile remained, bleeding profusely from the corner of its mouth. It dipped its bill in water and approximately 1 min later captured and ate a 12-cm bullhead.

On 19 May 1983 between 14:14 and 14:20 at Duck Lake, 12 km north of Creston, a second observed case of extreme aggression occurred. One adult heron (A) had just captured and eaten a 10-cm largemouth bass (*Micropterus salmoides*) when a second adult heron (B) flew toward it. As B approached, A flew 10 m in the opposite direction. B then landed 15 m from A and the two faced one another, both in aggressive upright postures. B turned and in a forward posture walked slowly away from A. A then followed, still in an aggressive upright posture. A turned and in a forward posture walked slowly away from B. B followed, still in a forward posture. B then flew and landed on the back of A. B struck four glancing blows at the head and neck of A, and with its mandibles grasped A's neck just below the head and held A's head under water for 5 sec. A freed itself from B's grasp whereupon B struck and hit A on the back. A then flew and landed about 150 m from B.

On another occasion we discovered a dead heron which we believed to have been killed fighting with another heron. At 08:00 on 11 January 1979, EM observed an adult Great Blue Heron standing near a small opening in the ice near the CVWIC and a dead juvenile heron in the snow 12 m away. The carcass had a punctured cranium and in the fresh snow were spots of blood, wing tip marks, and heron tracks. No signs of a predator's activities were found in the snow or on the carcass.

We believe these incidents of extreme aggression are related to limited access to foraging sites. Deep water in summer (Forbes and Flook, unpubl.) and ice in winter restrict the access of Great Blue Herons to their foraging sites and possibly intensify competition among herons. Adults feeding young in May and the presence of fledged young on the foraging grounds in July may also increase competition. Bayer (Natl. Audubon Soc. Resear. Rept. No. 7:213–217, 1978) found that juvenile Great Blue Herons in Oregon fed non-territorially and disappeared at a greater rate over winter than did adults. He suggested that territory acquisition was essential to over-winter survival. We believe that the intense aggression we observed resulted from a shortage of suitable foraging sites, and that the risk of serious injury during aggressive fighting perhaps explains the rarity of such behavior.

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Combined-effort hunting by a pair of Chestnut-mandibled Toucans.—Combined hunting efforts have been reported for many predatory birds, including Cattle Egrets (*Bubulcus ibis*) (Wiese and Crawford, Auk 91:836–837, 1974), Golden Eagles (*Aquila chrysaetos*) (Meinertzhagen, Ibis 14:530–535, 1940), Lanner Falcons (*Falco biarmicus*) (Mebs, Vogelweit 80: 142–149, 1959), Eleonora's Falcons (*Falco eleonorae*) (Walter, Eleonora's Falcon, Univ. Chicago Press, Chicago, Illinois, 1979), and Crested Caracaras (*Polyborus plancus*) (Whitacre et al., Wilson Bull. 94:565–566, 1982), with either of two general scenarios occurring: one

bird works as a "beater," flushing prey while another bird follows, ready to exploit any sudden appearance of prey, or two (or more) birds pursue the prey, either simultaneously or alternately. Observations of an individual of one species using a member of another species as a "beater" have also been made (Bourne, Ibis 102:136, 1960; Currie, Ibis 102: 475, 1960; for review see Rand, Fieldiana:Zoology 36:1–71, 1954).

The Chestnut-mandibled Toucan (*Ramphastos swainsonii*), occurs from Honduras to western Ecuador. It is said to subsist primarily on fruits but also preys opportunistically on insects, small reptiles and amphibians, and on the eggs and young of other birds. Although some observations of predation on insects, bird eggs, nestlings, and lizards have been reported (Laughlin, Condor 54:137–139, 1952; Koepcke, J. Orn. 113:138–160, 1972; Skutch, Publ. Nuttal. Ornith. Club, No. 10, 1972; Howe, *Ramphastos swainsonii,* pp. 603–604 *in* Costa Rican Natural History, D. Janzen, ed., Univ. Chicago Press, Chicago, Illinois, 1983), little information is available on actual hunting behavior. Here we describe observations of two Chestnut-mandibled Toucans preying on a lizard.

These observations were made on Barro Colorado Island, Panama, on 5 May 1983. We first observed the pair of toucans at 14:00, perched about 10 m away from us. After we had watched them for about 60 sec, one flew to a large silkcotton tree (*Ceiba pentandra*), touched its feet to the trunk, hovered momentarily and then returned to its perch 4 m away. Within 1–2 min, the other toucan flew towards the tree, flushing an *Anolis frenata* (about 30 cm long) which scurried down the trunk and halted under a large philodendron (*Philodendron* sp.) leaf. Four min later one of the toucans flew directly at this leaf, flushing the lizard onto the exposed trunk. As the lizard ran down the trunk, the second toucan, who had been watching attentively, flew towards the lizard and attempted to catch it with its bill. One toucan perched on a vine next to the tree trunk, while the other perched about 7 m away. For the next 3–4 min they both watched the trunk. Then the toucan perched 7 m away flew and brushed past the tree, again flushing the lizard from beneath a large leaf. As the lizard ran down the tree and onto the opposite side of the trunk from this toucan, the second toucan pursued the lizard in a spiralling chase down the trunk, finally catching it in its bill. The bird then flew to an understory perch and began crushing the lizard in its bill by means of a biting action. The second toucan flew to a perch only 3 m away from the first and watched. After 20 sec of biting, shaking, and occasionally beating the lizard against the perch, the lizard's tail fell to the ground. The nearby toucan immediately hopped and flew down to the forest floor, picked up the tail in its bill, and flew to another perch. By this time the first toucan had ceased shaking the lizard. As the second toucan swallowed the tail, it was joined by the first toucan, still carrying the lizard in its bill. After 1–2 min, the toucans departed together.

With but one observation of Chestnut-mandibled Toucan pair-hunting behavior, we can draw no conclusions about the intent of cooperation or lack of it. Several behavioral traits show their ability to cooperate, however, and suggest that cooperative hunting is possible. They are gregarious, mates preen each other, and often feed one another fruit (Skutch 1972). Well after breeding, males defend portions of fruiting trees against all other frugivores except their mates (Howe 1983). Hunting in pairs may increase the success rate in capturing elusive prey, as has been suggested for some of the other pair hunting birds mentioned above.

A question arising from these observations is whether or not both toucans getting a portion of the lizard was strictly a coincidence. Autotomizing of tails is an escape mechanism frequently used by lizards (Dial and Fitzpatrick, Science 219:391–393, 1983), and could be learned by predators. The behavior of the toucans, including the fact that shaking of the lizard stopped just after the tail fell off, suggests that the process was not new to them, although the possibility remains that it was unexpected.

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Brigham Young University, and thank the staff of the Smithsonian Tropical Research Institute, Barro Colorado Island, who provided facilities while we were in Panama. Alexander Skutch, Neal Smith, Burt Monroe, and Henry Howe kindly provided suggestions and comments on an earlier draft of this note.—David P. Mindell and Hal L. Black, *Dept. Zoology, Brigham Young Univ., Provo, Utah 84602.* *Accepted 19 Mar. 1984.*

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Birds predominate in the winter diet of a Barn Owl.—Barn Owls (*Tyto alba*) are thought to prey primarily upon small mammals (Marti, Condor 76:45–61, 1974; Hamilton and Neill, Am. Midl. Nat. 106:1–9, 1981; Bunn et al., The Barn Owl, T. & A. D. Poyser, 1982). This note describes an instance of a Barn Owl feeding primarily on birds. A single Barn Owl of unknown sex roosted in a barn on the Marais Temps Clair Wildlife Area, St. Charles Co., Missouri, from approximately November 1980–March 1981. The 373-ha area comprises a large riverine marsh surrounded by agricultural land.

Forty regurgitated pellets were collected from the barn in August 1981 and examined for identifiable remains. Skulls, feet, and feathers of birds, and skull, mandibles, and fur of mammals were contained in the pellets and were used to identify prey, primarily by comparing with museum specimens. Numbers of individuals consumed were determined by counting skulls or skull fragments within pellets. Biomass of each prey type was estimated from published weights (Marti 1974) and museum specimens.

Avian material occurred in 39 of 40 (98%) pellets and mammalian remains occurred in only four (10%). Remains of 21 Red-winged Blackbirds (*Agelaius phoeniceus*), four Starlings (*Sturnus vulgaris*), one Rusty Blackbird (*Euphagus carolinus*), one Common Grackle (*Quiscalus quiscula*), one *Microtus* sp., and one *Peromyscus* sp. were identified. Based on prey weight estimates (in parentheses) the relative contribution to diet biomass of these taxa was as follows: Red-winged Blackbird (60 g) 69.6%; Starling (80 g) 17.7%; Rusty Blackbird (65 g) 3.6%; Common Grackle (100 g) 5.5%; *Microtus* sp. (45 g) 2.5%; *Peromyscus* sp. (20 g) 1.1%. Birds comprised 96.7% of the food ingested.

Marsh areas of the Marais Temps Clair Wildlife Area were used by large flocks of "blackbirds" during winter 1980–81. Although Barn Owls typically feed on small mammals, their diets have been shown to shift to include more avian prey when rodent populations decline (Hawbecker, Condor 47:161–166, 1945; Otteni et al., Wilson Bull. 84:434–448, 1972; Smith et al., Great Basin Nat. 32:229–234, 1972). No studies in North America have documented a proportion of birds in the diet as large as that reported here. Lacking information on small mammal abundance, we don't know if the higher incidence of birds resulted from a decline in rodent populations or was simply a dietary response to a readily available concentration of marsh dwelling birds.

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ORNITHOLOGICAL LITERATURE

THE AUDUBON SOCIETY MASTER GUIDE TO BIRDING. Edited by John Farrand, Jr. Alfred A. Knopf Publ., New York, 1983, 3 Vols. In total, 1245 pp., 1438 full-color illustrations, 422 black-and-white drawings, 650 range maps. $13.95 per volume.—The Audubon Master Guide to Birding is described by its publishers as being "An advanced field handbook to the Birds of North America in Three Volumes." Its text is the work of 61 authors, all experts on certain taxa, habitats, or regions; together they have produced hundreds of species accounts in addition to summary descriptions of higher taxonomic categories and a number of special essays. The authors also advised on the selection of pictures used to illustrate each species, the majority of which are photographic. To represent infrequently photographed species, nine artists were commissioned to paint portraits of birds in their appropriate habitat. A total of 1245 photographs and 193 paintings are used to illustrate the 835 species which occur regularly in the United States and Canada, and for which full accounts are provided in the text; with all of this material, as well as a considerable amount of supplemental information, it is not surprising that three volumes are required.

In the front of each of the three volumes a brief description of the orders of birds covered in that particular volume is provided, as are drawings illustrating the parts of a bird and brief essays on "How to Use This Guide," "How to Identify Birds," and "How to Find Birds." (These later features are the same in each volume.) At the back of each volume, following the descriptions of species regularly occurring in North America, are brief accounts (unillustrated) of those species (belonging to the orders appearing in that volume) that have been recorded as accidentals in North America. A glossary containing terms used in each individual volume follows this list of accidentals, and is followed in turn by notes on the authors and artists (as well as a list of photo credits) who contributed to that volume.

In addition, a number of special essays are included. In Volume I, Kenneth Parkes has written a section on "Classification and Nomenclature," while in Volume II there are chapters on "Birding Equipment," "Reporting a Rarity," and "Rare Bird Alerts"; these last two provide information on what to do when and after you sight a rare bird, as well as how to learn if any unusual birds have been discovered recently in a specific area. Volume III includes an essay entitled, "Beyond Bird Identification," which provides a brief insight into scientific ornithological research. This last volume also includes a comprehensive index to all three books. (An index pertaining to its contents alone concludes each of the other volumes).

The arrangement and nomenclature of taxa throughout the set follows the new, 6th Edition of the A.O.U. check-list (A.O.U. 1983) which is, as the publishers note, "the sequence followed by professional ornithologists." Why this was done is not at all clear, since it is doubtful whether the majority of bird watchers—and therefore field guide users—own, use, or even refer to the official A.O.U. publication. As much as is possible, the ordering of genera and species in the check-list reflects what its authors feel to be the phylogenetic history of a given taxon, more generalized forms being described before the specialized types. In many cases of course, what are in reality branching patterns are arranged in some contrived, linear order. In addition, as the check-list committee admits, "in many cases, we lack sufficient evidence to make sound inferences" about the history of a taxon. In such cases they "followed the most widely used, conventional geographic sequence of species, with the roughly northernmost form listed first and the southernmost last, or from west to east if the division of ranges is more oriented to that axis." In other words, the ordering of taxa in the check-list is often arbitrary and can in no way be inferred to represent the final, let alone present, "truth" about the evolution of North American birds.

Regardless of its inherent taxonomic value, the official A.O.U. sequence seems particularly inappropriate for use in a field guide. How many bird-watchers, we wonder, really care about the supposed phylogeny of the individuals they are observing? More importantly, the use of this quasi-taxonomic order in the Master Guide leads to situations in which the pictures of very similar looking species are pages apart—a circumstance which does nothing to help "provide the vital information required during the few seconds a bird may be visible," as the Audubon authors assert (in the preface to each volume) that they wish to do. The photographs of Bald (*Haliaeetus leucocephalus*) and Golden (*Aquila chrysaetos*) eagles for example, are separated by 30 pages, while those of the Eastern Phoebe (*Sayornis phoebe*) and the Eastern Wood-Pewee (*Contopus virens*) are placed 18 pages apart; Townsend's Solitaire (*Myadestes townsendii*) and the Northern Mockingbird (*Mimus polyglottos*) are separated by 12 pages. The species in these pairs (as well as others) are cited by the Audubon authors as being similar in appearance and thus potentially confusing in the field; placing them on the same page, as is done in most of the other currently available guides; seems to better facilitate easy and rapid comparison in the field. This is a problem we find associated with both this and the earlier Audubon guide in contrast to most other field reference books; in this one, in fact, even pictures of the same species are often on different pages. Although this will not perhaps pose much of a problem for expert bird watchers who no longer find similar species confusing, tyros, and those of intermediate experience, may find themselves madly flipping pages while the bird under observation moves on.

Volume I of the set contains the Gaviiformes, Podicipediformes, Procellariformes, Pelecaniformes, Ciconiiformes, Phoenicopteriformes, Anseriformes, Falconiformes, Galliformes, Gruiformes and the shorebirds of the order Charadriiformes. Volume II concludes the Charadriiformes (with the gulls and terns and their allies) and continues on through the remaining avian orders with the exception of the Passeriformes, which is covered exclusively in Volume III.

In its turn, each family of birds is allotted a separate section, beginning with a general description of the family, and ending with a list of the members of that family found in North America. The text entry for each species then begins with the bird's scientific and English names, followed by a synopsis of the features most useful in identification of that species. Although the individual species accounts vary substantially in length, each typically contains a general description of the bird, including information on its appearance (including size, shape, etc.), habitat preferences, behavioral characteristics, and sometimes a brief description of its taxonomic history. The voice of all species for which the authors consider voice useful in identification is then described under a separate subheading, as are similar species, if any. Finally, the range of the species is discussed, including a description of its breeding and wintering ranges and a brief indication of its activities outside of North America. A map illustrating this information is provided adjacent to the relevant text for each species.

Full-color pictures of those species which occur regularly in North America (north of Mexico) appear opposite the text relating to them. Although in some cases a single picture was considered sufficient to allow identification, in others the extent of plumage variation with age, between the sexes or within the geographic range of the species, warranted the use of up to six illustrations. Adjacent to the picture is a small "plate key," or black-and-white reproduction of the plate, on which are superimposed red arrows corresponding to numbered field marks which are listed just below the key. Beneath the numbered characters, additional features, potentially useful for identification are sometimes given; these include size, shape, voice, or habitat preference. In some cases black-and-white drawings of flight postures or different plumages supplement the color plates. Many of the photographs used are excellent and often serve to illustrate, better than could a stylized portrait, the features that one would

really see and should look for while watching a particular species. Unfortunately, the use of photographs also incurs several disadvantages. Firstly, good pictures of a particular taxa or age class are sometimes unavailable; a number of the photographs used are thus poor and a few are inadequate by virtue of the lighting, lack of focus or positioning of the bird they display. Secondly, by their very nature, photographs lack standardization. Even within the portfolio of a single photographer, differences in type of film, lighting or the development process can alter the appearance of the same bird in a variety of ways, and when 203 different photographers are involved (the number that have contributed to the Master Guide), these problems are multiplied manyfold. The difficulties this can cause are particularly apparent when different plumages of the same species or very similar species are compared. On page 295 of Volume III for example, a distinctly orange Eastern Meadowlark (*Sturnella magna*) is pictured immediately above a more appropriately yellow-colored Western Meadowlark (*S. neglecta*). Although an expert birder will realize that this difference in hue is merely an artifact of the photographic process, novices may be lead, in this and other cases, to misidentify individuals they see in the field.

Where photographs were unavailable, paintings have been substituted. As with the photographs, many of these are excellent. Others, however, are less so; some of the works of J. E. Coe, for example, have an unusual yellowish tint which tends to misrepresent the color of certain species (e.g., Crissal Thrasher [*Toxostoma dorsale*] and Field Sparrow [*Spizella pusilla*]). Regardless of the quality, many of us found the interspersion of paintings (in nine different styles) and photographs (some overly dark and others badly blurred) esthetically irritating and would have preferred a more consistent system of representing species. The birds themselves are variable enough; introducing additional sources of variability does not aid the identification process.

The authors of this guide are to be congratulated for at least attempting to provide more details about seasonal, age-related and geographic plumage variation than have been presented in earlier guides. Unfortunately, for some taxa the choice of which details to present has perhaps not always been the wisest, while for others the discussion of variation is no more adequate than that found in previous guides. On page 181 of Volume III for example, the male and female Wilson's Warblers (*Wilsonia citrina*) are shown in separate photographs. The only difference between the sexes listed among the field marks is that the female rarely possesses the black cap which is characteristic of the male. Despite this comment, however, the individuals pictured are essentially identical, both showing a distinctly dark cap. In illustration of the second point, the very wide range of plumage variation shown by both first-year male and female Northern (Baltimore) Orioles (*Icterus galbula galbula*) for example, is not mentioned and the pictures shown are supposed to represent *the* type of these two age/sex classes. In fact, the appearance of females and young males overlaps extensively and it is impossible to determine with certainty the sex of a dull colored bird unless it is in the hand. In other cases, the races pictured to illustrate geographic variability within species seem in some cases ill-chosen or inadequate in number. There are the same number of pictures of the invariant Golden-crowned Kinglet (*Regulus satrapa*) for example, as there are for the Song Sparrow (*Melospiza melodia*), one of the most variable species in North America. And, of the two *melodia* forms represented, one is the Aleutian Island race which (a) is sympatric with very few species with which it might be confused, and (b) is likely to be seen by only a fraction of the field guide users in Canada and the continental United States. If only two races can be shown, why not one of the more common, and distinctly darker-colored, forms found in the continental West (e.g., *morphna* or *inexpectata*) plus one of the eastern or interior races (e.g., *melodia* or *juddi*).

Finally, one wonders if it was the number of photographs available that determined the length of the text or vice versa. Whichever, the end result is that one or the other categories

of description is sometimes inadequate. The Olive (*Peucedramus taenaitus*) and Prairie (*Dendroica discolor*) warblers for example each merit a full page of description, opposite three photographs. For the widely distributed Yellow-breasted Chat (*Icteria virens*), however, one picture is apparently sufficient, which limits the written text to a too-brief, ⅓ of a page. The system of allotment seems somewhat arbitrary.

As might have been expected when so many authors are involved, the quality of the text is uneven, with respect to both style and content. In places, the work is excellent. For the shorebirds in particular, the species accounts are full of useful information without excess verbiage. Frequently, however, a small increase in information over that contained in conventional field guides is obtained at the cost of adding many confusing modifiers and unnecessary sentences. What do the phrases, Ospreys (*Pandion haliaetus*) "hunt at moderate altitude," and are, "quite vocal," mean, for example (Volume 1:216)? What is "impressive size" (Volume III:224), and is it particularly helpful to learn that the vocalizations of the Black-legged Kittiwake (*Rissa tridactyla*) include "other gull-like calls" (Volume 2:78)? Particularly in the general family descriptions, the text becomes so vague as to be contradictory. Under the heading "Icterinae," we are told that, "the Meadowlarks—especially the Western—are rather good singers, unlike the rest of the members of this subfamily." Three sentences later, however, we learn that many orioles, also members of this subfamily are, "loud singers, capable of complex vocalizations." One wonders what qualifies meadowlarks then, and not orioles, as "good singers."

In addition, a fairly quick reading has revealed several errors in content. The range of the Olive Warbler is given as central and southeastern Arizona and southwestern Mexico (Volume 3:186), which should instead read, Arizona and southwestern *New* Mexico. The *princeps* race of the Savannah Sparrow (*Passerculas sandwichensis*) is described in two places as being found on "Cape Sable Island." It is actually resident on Sable Island, which is located 177 miles (283 km) off the coast of Nova Scotia. Cape Sable is a much smaller island, situated almost touching the southeast coast of the same province, or a place in Florida. In another place, the spicules on the bottom surface of an Osprey's feet are described as being "shiny," when probably "spiny," is meant (Volume 2:216). Just as serious are simplifications that sometimes serve to misrepresent the extent of knowledge about a particular taxon. We question, for example, the assertion that Northern Harriers (*Circus cyaneus*) detect prey "solely by hearing." One wonders how many other such typographical and contextual errors a more careful reading would turn up.

Elsewhere, details that could aid substantially in the identification of certain taxa are missing. Although a key diagnostic feature for the Lesser Nighthawk (*Chordeiles acutepennis*) (that the outermost primary is shorter than its nearest neighbor) is evident in one of the photographs provided, it is not mentioned in the text. Similarly, there is no description of the characteristic flight pattern of the Barn Owl (*Tyto alba*) (legs droop, labored flight, awkward manner), which is a useful feature for identifying the species.

The authors of the Master Guide have undertaken an ambitious project: to amalgamate in one publication what have in the past have been the separate responsibilities of (1) field guides and (2) more text-oriented handbooks dealing with the natural history of specific avian taxa or faunal regions. To this end they have tried to include more descriptive information on the appearance and life history of species and higher categories than have been available in previous field guides, while still attempting to preserve various features that make a book useful for field identification. Unfortunately , in many respects, the attempt has been less than successful.

For the several reasons discussed above, the Audubon guide presents serious problems for the less than expert bird watcher in terms of fulfilling the role of a field guide. Level of experience aside, the sheer size of the package makes the Master Guide less than appealing

as a field companion; each single volume weighs more than most standard field guides and the entire set tips the scales at 1.98 kg (4.4 lbs). In addition, the binding is not particularly field-worthy: the review copy has begun to break apart already after only 2 weeks of strictly desk use.

For an expert bird-watcher, many of the difficulties with the illustrations which have been discussed above will not pose much of a problem. Essentially, such individuals are much less dependent on a guide to make accurate and rapid field identifications. The guide does state that it is designed primarily, "to satisfy the demands of advanced birders." For these presumably, it is the increased amount of descriptive information that is supposed to make this guide of especial value. Yet, as we have described, there are problems with this aspect of the guide as well. The actual increase in information is at times less than substantial, and in places the text is in error; although expert birders are thus unlikely to be frustrated or lead astray by inadequacies in the pictures or range maps, it is a shame that the quality of the text, their major interest, is not uniformly higher.—N. J. Flood, G. R. Bortolotti, P. Fetterolf, E. Nol, C. Risley, J. D. Rising.

Les Oiseaux de Chine, de Mongolie et de Corée. Passereaux. By R. D. Étchécopar and F. Hüe, illus. by Patrick Suiro and Gilbert Armani. Société Nouvelle des Éditions N. Boubée, Paris, France, 1983: 705 pp., 21 color plates, 2 black-and-white plates, numerous text figures, 2 general and 350 distributional maps. French francs 450F.—Until the beginning of this century, Chinese zoology, as we understand it today, had been entirely in the hands of European scientists, even amateurs. The Chinese had long had their own way of studying living creatures, birds in particular, but it was entirely different from the modern trends of Natural History. Several British naturalists, particularly Swinhoe, a consul, and later on La Touche, a customs official, played an important part. The major contribution, however, was that of French travelers; we must mention the most important of all, Father Armand David, a missionary whose discoveries were sensational—among them Pere David's Deer (*Elaphurus davidianus*) and the Giant Panda (*Ailuropoda melanoleuca*). He was working in cooperation with Professor E. Oustalet, the Curator of Birds at the Paris Museum. A general work, in two volumes, "Les Oiseaux de la Chine," was the final result, and the first comprehensive study on the subject (1877). One should also remember the work of the French Jesuits at the University of Szi-Kawei, near Shanghai, who had built up considerable collections now, I am assured, preserved in Peking.

In more recent years two French ornithologists, R. D. Étchécopar and F. Hüe, have also become interested in the Chinese avifauna, after having published large books on the birds of Northern Africa (1964) and Western Asia (1970). Their first volume of "Les Oiseaux de Chine, de Mongolie et de Corée" was published in 1978 (609 pp.). The relatively long delay in the appearance of the second volume was due to the difficulties following the accidental death of F. Hüe and that of the illustrator, Paul Barruel. But R. D. Étchécopar has managed to overcome them and to offer us one more big book, with many plates and maps, which makes comparatively easy the identification of the numerous species of that very important part of the Old World known as the Far East, all the richer in species in that there are no considerable stretches of water or desert between temperate eastern Eurasia and the tropics of Indochina and Malaysia.

This second volume has, of course, no general chapters, but a selective bibliography (too restricted in my opinion) follows, with indexes of Latin, French and English names which prove to be very useful. The illustrations, of a practical type, are satisfactory, the great majority of them by Patrick Suiro. All of the essential information one expects to find in such a book is up to date and accurate, but one soon realizes how much remains to be

learned on the subject. A very useful feature is the large number of distributional maps, covering practically all the different species. Inaccuracies and omissions are at a minimum. This heavy volume will prove very useful to all interested in Asian avifaunas and constitutes a sound foundation for further studies.—JEAN DELACOUR.

JOHN CLARE'S BIRDS. Edited by Eric Robinson and Richard Fitter, illus. by Robert Gillmore. Oxford University Press, New York, New York, 1982: 105 pp. $16.50.—English poets of the Romantic period were frequently nature lovers. Their works abound with skylarks, nightingales, daffodils, and clouds, all of which easily become metaphors for poetic fancies. But John Clare (1793–1864) was more than a nature lover; he was a true naturalist, a close observer of everything that grew, flew, or moved in the area of his native village of Helpston, near Peterborough. Thus it is not surprising that when he writes about a Blue Tit (*Parus caerulescens*), for example, we are going to get facts about this bird:

The blue cap hid in lime kilns out of sight
Lays nine small eggs and spoted red and white

The details may include not just the number of eggs and their color, size, and shape, but where and how the nest is built, what the bird's flight is like, its song or call, whether it migrates, and any other distinguishing characteristics. It is the bird, not the poet, who is the focus of the poem. The bird's world is central, and the poet merely observes, and wonders. Yet because he is such a precise observer, that world is really brought before us; there is always excitement, things are discovered; we are there. Here is the Quail:

"I wandered out one rainy day
And heard a bird with merry joys
Cry wet my foot for half the way
I stood and wondered at the noise

When from my foot a bird did flee
The rain flew bouncing from her breast
I wondered what the bird could be
And almost trampled on her nest

The nest was full of eggs and round
I met a shepherd in the vales
And stood to tell him what I found
He knew and said it was a quails

For he himself the nest had found
Among the wheat and on the green
When going on his daily round
With eggs as many as fifteen

Among the stranger birds they feed
Their summer flight is short and slow
Theres very few know where they breed
And scarcely any where they go"

All precisely and economically noted: nothing could be more factual. Yet there is mystery too ("I wondered"); who can know where these birds come from, or where they go?

Clare's idiom was the vernacular of Northamptonshire, and his spelling was original; these editors have left things as Clare wrote them. (His earliest editors, it seems, felt no such

restraint.) Sometimes the effect is to sharpen the drama, as in this commonplace rural event, nest-robbing by schoolboys. The bird is a Chaffinch, or "pink," from its note:

"The schoolboys in the morning soon as drest
Went round the fields to play and look for nests
They found a crows but dare not climb so high
And looked for nests when any bird was nigh
At length they got agen a bush to play
And found a pinks nest round and mossed with grey
And lined about with feathers and with hair
They tryed to climb but brambles said forbear
One found a stone and stronger then the rest
And took another up to reach the nest
Heres eggs they hollowed with a hearty shout
Small round and blotched they reached and tore them out
The old birds sat and hollowed pink pink pink
And cattle hurried to the pond to drink"

The narrative moves swiftly until the last two lines, when the action shifts from the schoolboys to the birds in their helplessness, and then to the cattle, who, like a Greek chorus, comment on the little tragedy by retreating from it—the one word "hurried" being enough to make us catch our breath.

It is baffling to try to explain the appearance of a writer like John Clare. He seems almost a sport of nature, someone who, against all the logic of his origins, knew very early the unlikely thing he wanted to do, and proceeded against all the odds to do it. Clare was the son of illiterate agricultural laboring people: from the time he was very young he went out to work with his father, attending school for only three months in the winter each year until he was twelve. After that there were only a few classes with boys in the village, though he read unceasingly, whatever books he could find. When he was thirteen a village weaver showed him the "Spring" section from James Thomson's "The Seasons," and though it was his first encounter with poetry, he knew at once that that was to be his form. By the time he was sixteen he was writing constantly, or rather, lacking both paper and leisure, he shaped the lines by saying them aloud as he worked in the fields—"muttering," as he called it. He tested them on his parents, pretending he had copied it all from books; they listened and he found their responses helpful. If they were mystified he knew he must make things plainer; if they thought it foolish, that was useful too. He had no other critics.

In 1820 he published his first volume: "Poems Descriptive of Rural Life and Scenery." It was an immediate popular success; Clare was dubbed "the peasant poet," taken up by literary circles and made much of. But the celebrity seems to have been due more to the novelty of poetry appearing from such an unlikely source than to any real interest in the work itself; it did not last. He published three more books, none of which attracted much attention, nor did they earn any money, which was sorely needed. Married by now, and with seven children, his life was poor, harsh and mean, with strains and tensions that eventually drove him insane; he spent his last twenty-four years in the Northampton Lunatic Asylum. (The doctor who admitted him ascribed his condition to the "years addicted to poetical prosing.")

Clare is now ranked among the major poets of Britain. Studies about him appear with increasing frequency, and his work is to appear in a collected edition (Oxford English Texts), although it will be some time before this is completed. So far, Clare's work has been available mainly to specialists, and one hopes that this small collection of bird poems will make him more accessible. Eric Robinson and Richard Fitter say that they hope "to extend among

general readers an appreciation of Clare's sensitive response to birds," but for anything addressed to the general reader there are curious omissions indeed. We are not introduced to Clare himself—there is not the briefest of biographical sketches, not even—oh, most culpable editors—the dates of his birth and death. So that the otherwise useful discussion of Clare's work remains curiously suspended; there are no facts to connect it to. It seems probable that this edition was prepared by the English branch of the Oxford Press and carelessly flung at the American market as an afterthought. Do not be deterred, however. Once you have read this much, you will find yourself in the library anyway, for you will want to read more of this neglected and rewarding poet.—EDYTH S. MCKITRICK.

THE LIVING BIRDS OF ERIC ENNION. Introduction and commentary by John Busby, illustrations by Eric Ennion. Victor Gollancz/David & Charles, North Pomfret, Vermont, 1983: 128 pp., numerous sketches, pen-and-ink drawings, and watercolor paintings through text. $21.00—I must admit that before I received my review copy of this book I had never heard of Eric Ennion, but I now feel honored to have been introduced to his work! Most of the book is devoted to showing Ennion's art, and text is thus kept to a minimum. In his introduction, John Susby states that "Though he painted many hundreds of watercolours—landscapes and animals, as well as birds—the main purpose of this book is to show Eric Ennion's field sketches and small painting studies rather than larger finished works." "Finally there is a section on drawing and painting birds, based on Ennion's notes and teaching, which I hope will encourage all aspiring bird artists." These statements fairly well sum up the intent and content of the book.

Each of the seven chapters deals with a particular group, such as water birds, game birds, or open country and garden birds, and has an introductory statement and appropriate comments by Busby as well as quotes from Ennion's writings to accompany particular works.

Ennion is basically a watercolorist and his painting style is relaxed and loose. He is not a "tight" sketcher, but it is obvious that he is an extremely careful observer and he has that rare ability to put what he sees in the field onto paper with only those lines that count. There is no doubt about what a given bird is doing even if the sketch is of only a few lines and involves foreshortening or other "unusual" angles. I have looked through the book for hours and I still get pleasure and delight from looking at Ennion's birds; they may be loosely painted, but they are alive, with muscle, bone, and feathers. This "living" quality comes from hours of observation and hours of sketching with binoculars in one hand and pencil in the other, showing that one can only properly portray birds by knowing them. This field orientation is also revealed by the amount of bird behavior one sees in Ennion's work, such as among the group of 10 Oystercatchers (*Haemotopus ostralegus*) on page 40—they are resting, preening, calling, and scratching! Ennion's notes also often point out the behavior that he was observing when he made particular sketches.

Ennion's more finished works do not, at least to me, come off as well as his sketches. The finished pieces often have inked outlines and are somewhat "hard." A group of Siskins (*Carduelis spinus*) and Lesser Redpolls (*Carduelis flammea cabaret*) on page 97 and a Long-eared Owl (*Asio otus*) on page 57 both suffer from this "concentration."

On the other hand, studies of various warblers on pages 70–71, a dead Corn Crake (*Crex crex*) on page 122, two male Eurasian Robins (*Erithacus rubecula*) settling territorial boundaries on page 83, and Harlequin Duck (*Histrionicus histrionicus*) studies on page 28 are all soft and living.

Ennion has some good advice, gleaned from his years of work, for those who want to paint birds. One bit is especially useful—on page 119 he has a whole page of sketches of

"*Detailed* studies of feather tracts, alar folds & the surface muscle anatomy in a fledgling thrush found *dead* on the road after a storm. Such opportunities should not be missed if you hope ever to become useful at drawing the *live* bird." I echo his comments 100%—preparing specimens and sketching dead birds has been one of the most important things I have done to become familiar with how a bird is built, and I would urge every aspiring bird artist to at least get ahold of House Sparrows (*Passer domesticus*) or European Starlings (*Sturnus vulgaris*) to see how they go together. He also comments on how he sketches, and provides some ideas on a few useful watercolor techniques. One major criticism I have about what Ennion says is that he casually comments that any old paper will do, including the insides of envelopes or "school cartridge paper." Here I must take exception; why a person should work hard to produce outstanding work only to have it crumble out of existence in 50 years or less, I do not know. I would urge any young artist to work only with high quality materials; it is amazing how much better a good brush or a good piece of paper handles than does a poor one. It is obvious that Ennion often did his work on small pieces of paper and then assembled the pieces, especially when making a plate for a book. A group of warblers on page 70 looks as if they were done on scraps of envelopes and then glued onto a piece of paper bag or wrapping paper. I am glad they are reproduced in the book because I am sure that these lovely little sketches will soon be falling apart!

Since Ennion was British, his birds are those found in his native country, but his work will be of interest to most anyone with an interest in bird art. There are few, if any, "field guide" poses found among Ennion's birds and they are alive. I strongly recommend this book to anyone interested in the depiction of birds, and I also recommend it to anyone who enjoys just looking at a good selection of European birds that are shown "behaving in characteristic ways." I am quite sure that Louis Agassiz Fuertes and George M. Sutton would have both given a smile of approval to the work of Eric Ennion.—JOHN P. O'NEILL.

THE PLOVERS, SANDPIPERS, AND SNIPES OF THE WORLD. By Paul A. Johnsgard. University of Nebraska Press, Lincoln, 1981:493 pp., numerous black-and-white photographs and drawings, 60 color plates. $45.00.—Almost a century has elapsed since the publication of Seebohm's (1888) monograph on the plovers, sandpipers, snipes and their allies. In the intervening period a wealth of studies of shorebird biology has been published, but until the present book by Paul Johnsgard no one has attempted a modern synthesis. One of the principal reasons for this hiatus, I suspect, is the instability of shorebird taxonomy, which is due largely to uncertain relationships of such enigmatic groups as the jacanas, painted snipes, seedsnipes, pratincoles, coursers, sheathbills, thick-knees, and the Crab-plover.

Johnsgard addresses these problems only superficially in a short introductory chapter on taxonomy and evolutionary relationships, stating in the Preface that he used the recommendations of Bock (1958) and Jehl (1968) as his primary guidelines. Where no consensus existed or where he felt he had insights not shared by the rest of us, Johnsgard has instituted his own taxonomic judgements. Although the writing of a monograph allows the author license to do this, it is a deplorable practice which would not be permitted in the more rigorous peer-reviewed literature. The end result is that Johnsgard often manages to turn confusion into chaos at both higher and lower taxonomic levels, and in the process demonstrates his ignorance of the philosophy and practice of modern systematic methodology. For example, the "simplified phyletic dendrogram" (Fig. 1 in the book), depicting "evolutionary relationships of the tribes and genera of shorebirds," has a final bifurcation leading to the charadriids on one terminus and the scolopacids on the other. From this dichotomy

and a similar one in Fjeldsa (1977), Johnsgard concludes that the plover assemblage is generally more primitive and directly ancestral to the scolopacid assemblage. He clearly does not understand why a two-taxon hypothesis of relationships cannot possibly impute the primitiveness of either, and is unaware of the distinction between ancestor-descendent relationships and relationships by common ancestry (see Cracraft 1974).

In uncritically quoting McFarlane's (1963) contention that the Scolopacidae may be of more recent origin than the Recurvirostridae and Charadriidae because of their different sperm morphology, Johnsgard misinterprets the information provided by a derived character state. Sperm morphology of the Scolopacidae is evidence that they are a monophyletic group, not that they are of recent origin. Johnsgard also contends that the Ibis-bill (*Ibidorhyncha struthersii*) is most closely related to the stilt and avocet "line," but in Fig. 1 he gives it a more recent common ancestry with the oystercatchers than with the stilts or avocets.

The havoc wrought at lower levels of the taxonomic hierarchy is graphically illustrated by Johnsgard's treatment of a family with which I am most familiar, the Haematopodidae or oystercatchers. Taxonomic problems within this monogeneric family stem from the apparent convergence of morphometric form in species with widely separated distributions, the lack of a global view in assessing relationships, and the multiple origins of melanism in various species (Baker 1977). Having spent 16 years gathering data on all forms around the world, I am utterly amazed as to how Johnsgard could decide to recognize only five species. Despite the possession of yellow irides and pale flesh-colored legs by all forms in the Americas, Johnsgard has chosen to follow blindly Mayr and Short (1970) in restricting the American Black (*H. bachmani*) and Pied oystercatchers (*H. palliatus*) as subspecies of the European Oystercatcher (*H. ostralegus*). The latter, and all other species beyond the Americas, have scarlet irides and coral pink legs.

In his inconsistent treatment of the melanic forms, Johnsgard serves only to illuminate the pitfalls of "gut-feeling" taxonomy. He relegates the South African Black Oystercatcher (*H. moquini*) to a subspecies of the pied *H. ostralegus* (despite an average 150 g difference in body weight, and substantial morphometric and behavioral differences), but assigns separate species status to the Blackish Oystercatcher (*H. ater*) of South America, the Sooty Oystercatcher (*H. fuliginosus*) of Australia, and the Variable Oystercatcher (*H. unicolor*) of New Zealand. The recommendations of the New Zealand Checklist Committee (1970) and Baker (1974) to raise the Chatham Island Oystercatcher (*H. chathamensis*) to a full species are ignored as Johnsgard returns it to *H. o. chathamensis* as in Peters (1934). The unjustified lumping of morphologically diverse and geographically widespread species under *H. ostralegus* encompasses the range of variation for all other species as well! All this muddling simply serves to underscore what taxonomists have long maintained: good taxomony is a fundamental prerequisite for all comparative studies of related taxa.

The taxonomic section is followed by a short but interesting chapter on reproductive biology, with an appropriate emphasis on variations in mating systems. Then follows a key to the Families, Subfamilies and Tribes which Johnsgard chooses to recognize. The rest of the book is composed of treatments of individual species, organized within Family sections. The format follows Johnsgard's (1978) earlier book on "Ducks, Geese, and Swans of the World" by the same publisher. I profess my admiration for the industry of the author in pulling the diverse literature together for each taxon, and for the countless hours that he must have spent in penning all the sketches of species which are scattered through the text. The color plates are sometimes of poor quality and better separations of most species could easily have been obtained.

When a book of this scope is written by a non-specialist we might expect errors of omission and commission to occur, and this is indeed a failing of Johnsgard's text. For example, the breeding distribution of the Masked Lapwing (*Vanellus miles*) in New Zealand is hopelessly

out of date; this species now breeds widely in both major islands as a cursory glance at issues of "Notornis" in the last 5 years readily discloses. The Collared Plover (*Charadrius callaris*) has never been found breeding in Panama, the breeding range of the Piping Plover (*C. melodus*) is more extensive around the Great Lakes, the Killdeer (*C. vociferus*) breeds in Newfoundland (Strauch 1971), and the North American inland breeding range of the Sandplover (*C. alexandrinus*) is mapped inaccurately. Work on the White-fronted Sandplover (*C. marginatus*) by Summers and Hockey (1980) is ignored as is the pertinent paper by Strauch and Abele (1979) on the ecology of three species of plovers in Panama.

Perhaps the biggest disappointment of the book is the absence of summary chapters on population dynamics, foraging ecology, or migration and molt, topics of great moment in contemporary shorebird biology. Johnsgard claims lack of space for these omissions, but lack of time and expertise seem more likely reasons. While it is impossible to write an error-free text for such a diverse group of birds, it is inexcusable for the author not to have sought critical appraisals on various sections from known specialists in the field. In summary Paul Johnsgard's initial perception that the shorebirds were much too large and complex an assemblage for him to challenge is borne out by this book. However, despite its limitations most ornithologists interested in shorebirds will want to own a copy as a starting point for more detailed investigations. Perhaps the greatest value of the book is the stimulation it will undoubtedly provide to shorebird biologists to write a more authoritative text to replace it.—Allan J. Baker.

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SEABIRDS, AN IDENTIFICATION GUIDE. By Peter Harrison, illus. by the author. Houghton Mifflin Company, Boston, Massachusetts, 1983:448 pp., 88 color plates, 312 range maps, 31 numbered text figs. $29.95.—Because seabird-watching and the study of seabird biology form, respectively, an art and a science different in technique from their terrestrial counterparts, a promising niche has always existed for a good seabird identification guide. Seabird faunas are not adequately embraced by the continental or subcontinental scope of standard field guides. Thus seabirds are uniquely deserving of specialized worldwide treatment. W. B. Alexander's 1928 masterpiece, "Birds of the Ocean" (G. P. Putnam's Sons, New York and London) is today tainted only by its half-century-removed data set (only meagerly improved for many species in the intervening years), its correspondingly obsolete taxonomy, and its lack of that sine qua non of the modern field guide—abundant color plates (it had, in fact, none). In 1978 G. S. Tuck and artist H. Heinzel produced the rather quaintly titled "Field Guide to the Seabirds of Britain and the World (Collins, London)." At last virtually all species were illustrated in color, often in two to several plumages, and range maps were provided for all species. But closer inspection (see, for example, reviews in Auk 97:908–909, 1980, and in Ibis 121:532–533, 1979) revealed substantial flaws in the plumages and shapes of many of the birds pictured, along with numerous inaccuracies in the range maps and range descriptions. Most disappointing to us was Tuck's text, which frequently showed little advance beyond Alexander's. Its reviewers agreed that Tuck and Heinzel's massive effort was a welcome and generally commendable first step toward a modern, worldwide seabird guide. Now the state of the art has taken a quantum leap with the publication of Seabirds, An Identification Guide.

Peter Harrison's book, the product of seven years of intensive field research and a crash course in bird illustration, immediately invites comparison with Tuck and Heinzel's. But although Harrison emerges a clear victor, it is only fair to point out that the two projects were carried out under very different publisher's constraints. Tuck and Heinzel produced a very standard field guide with an abbreviated text, a 5" by 7.5" page format, rather small figures crowded onto 48 plates, and a grand total of 292 pages. The very title "field guide" emphasizes the book's handy 'field' accessibility, for which the thoroughness of a handbook is sacrificed. By contrast, Harrison's book is of the "identification guide" genre, along the lines of P. J. Grant's Gulls, A Guide to Identification (T. and A. D. Poyser, Calton, England, 1982). Its 448 pages are roughly 6" by 9", and its liberally illustrated subjects are found on 88 color plates. The plates and text treat virtually all known plumages. This results, for example, in a total of 98 individual frigatebirds figured, all labeled as to age and plumage (Tuck and Heinzel illustrate 13). Other comparisons to T & H might include albatrosses (118 vs 40) and stercorariines (37 vs 9). It is axiomatic that the development of field identification skills requires an appreciation of variation, be it by age, sex, season, geographical locality, etc. The "identification guides" (e.g., Harrison's) address this variation to a degree that the standard field guides simply cannot. Add to this Harrison's extensive treatment of identifying characters other than plumage (shape, flight, expression, and a number of other things which add up to what is repeatedly and annoyingly referred to as "jizz"), and you have far more than a field guide.

After the obligatory Roger Peterson forward is a brief introduction that summarizes the types of identifying characters which seabirds show and serves as an introduction to the components of the species accounts. Following this are the color plates with extensive facing-page identification notes. Just over 200 pages of main text follow the plates; species accounts run from ¼ to 2 two-column pages, and there are very useful introductions to orders, families and genera. Finally, after a token and not very helpful treatment of "sea-ducks" (a third of a page of text and three black and white plates), there is a section of range maps, 10 to a page, treating all 312 seabird species. The three major sections of the book are cross-

referenced. End cover maps show major breeding island groups (alas, Christmas Island has been displaced some 3500 km eastward in the Pacific Ocean!).

The plates were all painted by the author, thus avoiding the artist-author "communication gap" which plagues some guides. In general they are quite good, although certainly uneven. Harrison handles some groups very well (e.g., most gulls, terns, cormorants, sulids and petrels) and some rather poorly (loons, most storm-petrels, many alcids and some shearwaters). The plates of the "Pacific storm-petrels" (plates 35–36) are perhaps the poorest. But then storm-petrels typify many seabirds in that their instantaneous shapes ("snapshots") are at once very difficult to portray and of little use in identification. Harrison's text accounts of storm-petrel flight and "jizz" (more important to field identification) are excellent.

The bills of some loons and grebes, e.g., Red-throated Loon (*Gavia stellata*) and Eared Grebe (*Podiceps nigricollis*) have an exaggerated uptilt. The first-winter Red-throated Loon is too contrasty—it should show a gray wash over the sides of the neck to the throat. Five figures of (apparently) adult MacGillivray's Petrels (*Pterodroma macgillivrayi*) are shown, though the bird is known from only one specimen—a juvenile. The Short-tailed Shearwater (*Puffinus tenuirostris,* plate 30) is misshapen and too pale and gray, while the Buller's Shearwater (*P. bulleri,* plate 28) is too brown. The Western Gull (*Larus occidentalis,* plate 57) labeled "3rd-winter" appears to be a second-winter bird. It is odd that no first-winter (=first-basic) Herring Gull (*Larus argentatus*) is figured, even though this is a common plumage of an abundant northern hemisphere gull. Far too few of the alcids are shown in typical on-the-water posture, and the wings of several flying alcids are oddly long and thin. Readers will undoubtedly have found many other errors of omission or commission in the plates, but the overall results are excellent for a book of this scope. Within major groups (families, genera, subgenera) species are often grouped on the plates geographically—thus there are plates of South American gulls, Pacific storm-petrels, Atlantic auks, etc. In some cases the results are strange, e.g., Horned Puffin (*Fratercula corniculata*) being placed with the murres rather than with the very similar Atlantic Puffin (*F. arctica*) or with the sympatric Tufted Puffin (*Lunda cirrhata*). In most cases the groupings do make sense, and again we should point out that there is liberal cross-referencing.

Species accounts cover dimensions (length and wingspan), soft part colors, general characteristics, plumage descriptions, and sections on "flights, habits and jizz," "distribution and migration" and "similar species." There is, not surprisingly, a distinctly British tone to the text, and British names are listed first (perpetuating the deplorable practice of unmodified names such as "Guillemot" and "Shag"). Most British in flavor, and in many cases most valuable, are the sections on "flights, habits and jizz." British identification guide authors have been singularly successful in conveying "gestalt" characters and Harrison is no exception. These characters can be especially important among seabirds, which are often viewed at great distances and under unstable conditions. Thus we read on p. 345 of the Great Black-backed Gull (*Larus marinus*) that the ". . . fierce expression and barrel chest imparts more menacing jizz than congeners." Quite British, quite subjective, and, to those who have seen the species, quite correct.

The text approaches "handbook" proportions in its thoroughness. Descriptions are presented for all distinct plumages and extensive comparisons between similar species are given. The detail and apparent accuracy of the text is attributable not only to Harrison's talent and field experience but to the pre-review of the text by seabird specialists throughout the world and to the use of a tremendous body of references (some 300 citations are listed). In addition to a gem of an identification guide, Harrison has presented the eager seabird enthusiast with an important introduction to the primary literature. Untested field characters and other gaps in our knowledge of seabird biology are pointed out and offer a challenge to the guide's users.

While the book is not free of typographical errors, e.g., *L. a. vagae* (p. 344), Xantu's (p. 400), Ballearic (p. 421), and Dalmation (p. 424), those found were quite minor. Workers in western North America will be disappointed that the Yellow-footed Gull (*Larus livens*) is not figured and is barely described; for a detailed identification treatment see McCaskie (Western Birds 14:85–107, 1983).

The difficulties of mapping bird distributions in general, and seabird distributions in particular, are acknowledged, and Harrison's efforts are a qualified success. The map key (located at the end of the map section) contains three rather confusing categories, corresponding to three degrees of shading on the maps. "Breeding islands/areas" is straightforward, but the distinctions between the other two categories, "Breeding and non-breeding range" and "Migratory range" are vague and nowhere explained (nor are the arrows which appear on many maps). The only alcid for which a "Migratory range" is shown is the "Little Auk" (=Dovekie [*Alle alle*]); don't other alcids "migrate" as well? The "Migratory range" of the "Black-throated Diver" (=Arctic Loon [*Gavia arctica*]) is shown to include not only the west coast of North America south of Alaska, but the western two-thirds of the interior United States as well. Middle and South American ranges of Red (*Phalaropus fulicaria*) and Red-necked (*P. lobatus*) phalaropes are shown as "Migratory ranges," while that of the Wilson's Phalarope (*P. tricolor*) is called "Breeding and non-breeding range." The maps, while not always showing the complex and protracted movements of seabirds to best advantage, are generally accurate and form an excellent quick reference. Slight registration problems force many pelagic species "onshore," sometimes greatly so (see, for example, map of Sooty Tern [*Sterna fuscata*]), but the intended distributions are usually clearly shown. We should point out that the text accounts of distribution are detailed and excellent, with much recent information incorporated.

In summary, Seabirds, An Identification Guide, is a thoroughly modern and painstakingly crafted work which goes further than any other single volume in achieving its goal—the accurate identification of seabirds by the reader. It is a model "specialty guide" with a wealth of information. Because of the volume of information presented, "Seabirds" will undoubtedly yield many more minor flaws than we have pointed out, but the overall verdict is still a hearty recommendation.—Kimball L. Garrett and Ralph W. Schreiber.

Proceedings of the Symposium on Birds of the Sea and Shore. By J. Cooper (ed.). African Seabird Group, Cape Town, South Africa, 1981:474 pp. S.Af. Rd. $25.00.—The African Seabird Group held an international symposium on birds of marine habitats in November 1979; these proceedings were published in 1981. The volume contains papers on such a wide range of subjects that anyone interested in birds in marine environments should find something relevant. Twenty-seven papers are included, with abstracts of 10 more, and summary remarks by Ralph W. Schreiber.

The papers and abstracts are organized into five subjects, Feeding Ecology (10 titles), Patterns of Distribution (8 titles), Distribution Studies (6 titles), Conservation of Species and Habitats (6 titles) and Physiology and Breeding Biology (7 titles). As expected, the quality of the work varies greatly. Less expected, perhaps, is the lack of correlation between quality of the papers and prominence of their authors.

The Feeding Ecology section is the strongest part of the book. Robert Furness leads off with a fine contribution on interactions of seabird and seal populations with fish stocks, correlating major changes in bird populations with changes in commercial fishing practices. Robert Crawford and Peter Shelton try to do the same thing for South African bird and fish populations, but because fewer data are available the results are less clear. In a paper on

albatrosses and petrels as squid predators, M. J. Imber and A. Berruti present important insights on biogeography and behavior of the squids as well as the birds. The birds feed extensively at night and catch mainly those squid with a diurnal migration and with photophores. Imber also contributed a paper on diets of prions (*Pachyptila*) and of the storm-petrels *Pelagodroma* and *Garrodia*. *Garrodia* specializes on the cyprid larvae of the pelagic barnacle *Lepas australis*, while *Pelagodroma* eats a variety of larval fishes and pelagic crustaceans (Euphausiids and Amphipods are most prominent). Among the prions a nice negative correlation exists between bill width and prey size, although the Fulmar Prion (*P. crassirostris*) may specialize on adult *Lepas* barnacles.

The Patterns of Distribution section begins with a review by W. R. P. Bourne of physical factors affecting seabird distribution. The search for general rules and patterns is an important part of science, but the results in this case range from the trite to the improbable. Bourne betrays a surprising lack of understanding of oceanographic and meteorological processes, and the coverage of the relevant seabird literature is inadequate. R. K. Brooke presents a South African perspective on seabird and marine zoogeography. His classification of bird groups according to water temperature zones inhabited is interesting but adds little to Murphy's (1936; Oceanic Birds of South America) discussion of the same subject. A. M. Griffiths discusses biases in seabird census techniques and proposes a standardized method. Seabird biology will benefit greatly when its practitioners realize that different research goals (e.g., distribution, density estimation, diurnal activity patterns) are best approached with different census methods tailored to their specific statistical requirements. The rest of the "Patterns" section is devoted to reports of distributional observations in various parts of the southern ocean; these will be valuable to compilers of distributional works.

The Distribution Studies section is highlighted by J. Mendelsohn's observations of *Pachyptila* movements with weather systems at Marion Island. J.-F. Voisin and M. N. Bester report that the giant-petrels breeding at Gough Island are Northern Giant-Petrel (*Macronectes giganteus*) rather than Southern Giant-Petrel (*M. halli*), and point out some problems with the species separation. M. Waltner and J. C. Sinclair provide a nice analysis of distributional, mensural, and molt data obtained while banding Terek Sandpipers (*Xenus cinereus*). I found the descriptions of molt most interesting.

The Conservation of Species and Habitats section begins with a description of the most successful rehabilitation program for oiled birds (Jackass Penguin [*Spheniscus demersus*]) in existence. Then M. Gochfeld provides a narrative of the effects of a pipeline on nesting Common Terns (*Sterna hirundo*). The four remaining papers all are attempts to classify shorebird habitats according to patterns of use by the birds (two are from South Africa, two are from Europe).

A. J. Prater begins the Physiology and Breeding Biology section with a review of primary molt in palearctic waders. He tries to explain differences in molt schedules by differences in migration patterns, sex, size, and other aspects of life history. I wish that he had paid more attention to the systematics of the birds. How closely, for example, is the size-related variation in occurrence of suspended molt and partial molt of sandpipers paralleled in the plovers? Phenology of penguins is featured in two papers (R. M. and B. M. Randall on *Spheniscus demersus*; A. J. Williams on the Gentoo Penguin [*Pygoscelis papua*]). Sheila Mahoney presents a nice laboratory comparison of the thermal physiology of *Anhinga anhinga* and one species of cormorant (*Phalacrocorax*), concluding that physiological constraints are sufficient to explain the restriction of *Anhinga* to tropical and subtropical regions.

All in all, this collection should contain something of value for anyone interested in seabirds or shorebirds, but I suspect many readers will find a minority of the papers relevant to their own interests. I recommend it for all libraries, and for individuals interested particularly in seabird feeding ecology and shorebird habitat selection.—Wayne Hoffman.

WHISTLING DUCKS: ZOOGEOGRAPHY, ECOLOGY, ANATOMY. By Eric G. Bolen and Michael K. Rylander. Special Publications of The Museum, No. 20, Texas Tech Press, Lubbock, Texas, 1983:67 pp., 10 black-and-white figures, paper cover. $12.00.—The eight species of whistling-ducks, genus *Dendrocygna,* constitute a distinctive group usually classified apart from other anatids as a separate subfamily or tribe. This general review of their biology concentrates on distribution and zoogeography, comparative ecology, and morphology. The latter aspect emphasizes the skeletal and muscular systems in relation to feeding and locomotion. There is also a brief consideration of evolutionary relationships within the group. Persons interested in the whistling-ducks either from the standpoint of general biology or wildlife biology should find this work of great interest.—R.J.R.

THE GROUSE OF THE WORLD. By Paul A. Johnsgard. University of Nebraska Press, Lincoln and London, 1983:413 pp., 51 color plates, 72 black-and-white plates, 15 distribution maps, 31 numbered text figs., 24 tables, 3 appendices. $42.50.—This is an updated edition of Johnsgard's (1973) Grouse and Quails of North America, minus the material on quails but plus information on the Eurasian species of grouse, making the coverage of grouse worldwide. Not surprisingly, the format and organization of the two treatises are very similar. This book is also subdivided into two major sections: "Comparative Biology," containing 10 chapters (one new one on physiological traits), and "Accounts of Individual Species" including the nine North American species considered in the 1973 book plus seven Eurasian species.

The first section of this book is largely a repeat of the 1973 edition. There has been some reorganization and updating of the material with the inclusion of a new chapter dealing with such topics as digestion, sound production, physiology of moult, and circulatory adaptations, some of which appeared previously in the chapter on physical characteristics. Unfortunately statements such as ". . . [clutch size] has recently been discussed by Lack (1968)" remain in the text—recent in 1973 but hardly in 1983. Nevertheless this section provides an overview of what is known about the biology of grouse and, as such, it also provides students of this group of birds an effective entry into the literature.

The second section of the book deals with each of the 16 presently-recognized species of grouse, describing their taxonomic status, measurements, identification, field marks, age and sex criteria, distribution and habitat, population density, habitat requirements, food and foraging behavior, mobility and movements, reproductive behavior, and evolutionary relationships. To do this, it is obvious that Johnsgard has had to pull together a voluminous and often scattered literature (about 350 entries repeated from the 1973 book plus another 300 from the European and post-1973 North American sources); its compilation into one publication is a great service to tetraonid specialists as well as ornithologists in general. The photographs, many of which appeared also in the 1973 book, are generally of high quality and add considerably to this publication.

In my opinion, however, this book is disappointing from a number of viewpoints. Johnsgard has provided us with a review of the published (and unpublished) literature on the Tetraoninae but his is a very uncritical review and, at times, a review that perpetuates unsubstantiated conclusions as well as unexplained contradictions. For example, Johnsgard uses the term promiscuous ("complete promiscuity"—p. 47, "highly promiscuous"—pp. 52 and 67) in reference to the mating strategy of those species not obviously monagamous (bigamous or trigamous) or polygynous (lekking forms). Yet, to my knowledge, there is no evidence at all for such a mating strategy in grouse—it is purely an assumption. Likewise, subjects such as population density, clutch-size, food habits, and the like include a plethora of data for which the variability is so great as to render them virtually meaningless. If such

variation actually exists, of what value is it when documented in vacuo? For example, population densities are given for each species, yet they are provided without any reference to habitat heterogeneity (crude vs ecological density) and often without reference to season.

A second disappointment stems from the incomplete use of the post-1973 literature. Much of the recent research on grouse, at least in North America, has attempted to address many of the questions implicit in Johnsgard's first book on this group of birds; unfortunately, the questions remain but many of their recent explanations go unmentioned, at least for the species with which I am most familiar—Spruce (*Dendragapur canadensis*), Blue *D. obscurus*), Ruffed (*Bonasa umbellus*) and Sharp-tailed Grouse (*Tympanuchus phasianellus*).

This publication is also marred by unfortunate lapses on the part of the proofreader and mapmaker. For example, how many species make up the Phasianinae (p. 5), 151 or 155? The table indicates 206 species in the Phasianidae but, depending upon which figures one uses, there are either 209 or 213. The listing of hybrids (p. 50) is made unintelligible through the misalinement of data across the table. The range maps of Blue, Spruce, Black (*Lyrurus tetrix*, and Sharp-tailed Grouse and Willow (*Lagopus lagopus*) and Rock (*L. mutus*) Ptarmigan show subspecies ranges in places that do not agree with the text, lack symbols on the maps that are in the figure titles or vice-versa, and, in the case of Black Grouse, show a map inset without explanation. The phylogenetic tree (p. 4), which reflects Johnsgard's ideas on grouse phylogeny, appears to try to combine time and habitat on the same axis. The result seems to suggest that all six grouse genera evolved in grasslands and sagebrush, which contradicts the text. Furthermore, I question the validity of placing the Spruce and Sharp-tailed Grouse closer to the Blue Grouse than to the ptarmigans, for in my opinion, they are much closer to the latter than the former both morphologically and behaviorally, being essentially woodland ptarmigan.

In sum, this book, although an admirable compilation of the literature on grouse of the world, is by no means the last word on grouse biology.—D. A. Boag.

Owls of Europe. By Heimo Mikkola, illus. by Ian Willis. Buteo Books, Vermillion, South Dakota, 1983:397 pp., 8 color plates, 75 photographs, 42 numbered text figs., 69 numbered tables. $40.00.—This ably written book consists of three parts. "Special characteristics of owls" covers 36 pages and includes the origin of owls, taxonomy, anatomical characters, external features, some unique aspects of the owl physique, and owl pellets. I was surprised to learn that the soft fringe of the flight feathers may be less important to silent flight than is generally supposed. "Removal of this fringe made no difference to the wing noise of the Tawny Owl," but still this feature is presented in Fig. 2 as "an aid to silent flight." Part two covers "species descriptions," accounts of each of 13 regularly breeding species of Europe and four additional species "from countries adjoining the Mediterranean, some of which species may occasionally occur in Europe." Each species account contains the following sections: description, in the field, voice, behavior, food, breeding biology, and distribution. "In the field," usually the shortest section, presents general characteristics; sections on behavior, food, and breeding biology are usually the longest. Part three covers 50 pages and deals with "ecological relationships in European owls" under the headings of sexual dimorphism and differences in diet, prey relationships, ecological isolating mechanisms, and legal status.

The color plates by Ian Willis beautifully and lovingly portray the 17 species and their subspecies, as well as differences related to sex, age and color phase. There are 26 birds in perched pose; in addition, 23 forms are depicted in flight, a feature that shows the upper

body and spread wing plumage—an interesting aspect. Also, underwing plumage is shown for 11 species or subspecies.

There are more than 50 line drawings by Willis scattered throughout the text. Sketches at the beginnings of chapters show owls in typical habitats; it is here that Willis shows his full artistic ability.

The 75 black and white photographs (by 29 photographers, including the author) show features of 17 species of owls; there are flight shots, birds at the nest, photos of concealment posture, eggs and young.

The author has a good grasp of the literature, both European and New World. There is a "selected bibliography" (three pages), and a complete list of references (27 pages). Mikkola's involvement with owls is demonstrated by the 43 titles under his name (1968–72).

Sixty-nine tables, which follow the references, provide details of topics such as early fossils, wing-loading, pellet sizes, nesting sites, clutch size, brood size, wing lengths, mortality factors, population sizes, and, especially, food.

Of the 17 species of "owls of Europe," seven occur in North America; accounts of these birds may be of special interest to North American readers. The species accounts include 34 maps; these show for each species usually the worldwide and European breeding range. The author acknowledges the assistance of 73 ornithologists in the preparation of these maps. This widespread contact with other workers exemplifies the thoroughness with which Mikkola has addressed himself to the owls of Europe. Every owl watcher will want to own a copy of this book.—Robert W. Nero.

Redwings. By Robert W. Nero. Smithsonian Institution Press, Washington, D.C., 1984: 160 pp., 10 color plates, 30 black-and-white photographs, 10 diagrams, and 20 line drawings by James Carson. $22.50 cloth, $10.95 paper.—Robert W. Nero's two papers on the behavior of Red-winged Blackbirds (*Agelaius phoeniceus*), which appeared in 1956, must rank among the most widely cited studies ever published in the Wilson Bulletin. Now, after an absence of many years from the field of redwing research, Nero has produced an entire book on redwing behavior. Although based in large part on the same studies that led to the 1956 papers, the book nevertheless contains enough new observations and insights to make a valuable contribution to the scientific literature. At the same time, Nero writes with an engaging and lively style, which should make the book attractive to a popular audience.

On the subject of Red-winged Blackbirds, Nero is a true enthusiast. As early as the first page of the introduction, he reveals his status as a partisan by referring to the song of the male as "melodious." Nero's enthusiasm for his subject is coupled with impressive talent as an observer. Red-winged Blackbirds are one of the most thoroughly-studied of avian species, yet many of Nero's observations, at least to my knowledge, have still not been duplicated. For example, he gives fascinating descriptions of the performance of symbolic nest building by male redwings outside of the period of courtship and pair formation. According to Nero, such behavior occurs in contexts that indicate the male may be seeking to reassure the female, as when the nest has been disturbed and the female is reluctant to return. Another example of novel observations is Nero's descriptions of associations of siblings with each other and with their parents lasting long after fledging. In one instance, Nero observed two color-marked siblings still accompanying one another, and still begging from their male parent, more than three weeks after the young had left the nest, and after all three had left the breeding territory.

If Nero is at his best in describing his own careful observations, he is weakest in discussing

the results of more recent behavioral and ecological studies. Coverage of such studies is far from comprehensive, but then Nero intends his book to be a popular work and "not a technical paper or a complete survey of the Redwing literature." A more serious criticism is that Nero oversimplifies or distorts some of the complex evolutionary issues that he does choose to discuss. For example, at one point Nero suggests that polygyny in redwings is explained by the fact that first year females breed while first year males do not. The possibility that delayed maturity in males is a consequence rather than a cause of polygyny is not considered, nor does Nero discuss more realistic explanations for the evolution of polygyny, such as the polygyny threshold model and its alternatives.

The general plan of the book roughly follows a redwing seasonal cycle. After some introductory material, Nero starts the cycle at the onset of breeding. He describes male and female display behavior, male territoriality, courtship and pair formation, and nesting and parental care. He then more briefly considers the molt, flocking, and roosting. A final chapter discusses redwings as an economic and social pest. Throughout, the book is illustrated with marvellous black-and-white and color photographs and line drawings, which considerably enhance the descriptions of behavior. In sum, Nero has provided a useful and entertaining introduction to the natural history of Red-winged Blackbirds.—William A. Searcy.

Illinois Birds: Wood Warblers. By Jean W. Graber, Richard R. Graber, and Ethelyn L. Kirk. Illinois Natural History Survey Biological Notes No. 118, Illinois Natural History Survey, Champaign, Illinois, 1983:144 pp., 125 numbered text figs., 46 tables. Price not given. (available from: Chief, Illinois Natural History Survey, Natural Resources Building, Urbana, IL 61801).—This, the ninth and largest, most ambitious, publication in the series by the Grabers and Kirk on the birds of Illinois treats the wood warblers (Emberizidae, Parulinae). It begins with an introduction that describes the sources of published and unpublished data that the authors have used to compile the species accounts, as well as the methods they employed to collect original data. The carefulness of the authors' evaluations of species' records is exemplified by their recommendation (p. 26) that a published sighting of Bachman's Warbler (*Vermivora bachmanii*) in 1958 in southern Illinois be discounted, a sighting that was made by the authors themselves. Following the introduction are accounts of 43 species that have been reported to occur in Illinois, plus records of hybrids of Golden-winged (*Vermivora chrysoptera*) and Blue-winged (*V. pinus*) warblers.

For each species that breeds in Illinois, there is a general range map showing the breeding and winter distributions north of the equator. Each account also includes a figure depicting census results and the span of egg-laying dates in Illinois, a large map with breeding-season records for each county in Illinois, tables summarizing the results of population censuses in Illinois, and photographs or drawings of an individual of the species and, sometimes, its nest. The data presented in the text of each species account are typically subdivided into sections on spring migration, breeding, and fall migration. When additional information, such as clutch-size, is available from Illinois, it is included in the text, as are sections on winter records, specimens, and food habits. One feature of these species accounts that merits further comment is the excellent quality of the maps. The maps depicting breeding records in Illinois are large and the borders and names of counties are clearly identified. Their value is enhanced further by the use of symbols that code the records as having been from before 1900, from between 1900 and 1949, and from 1950 or later. The symbols are also coded into categories representing records of nests or young (i.e., confirmed breeding records) or June records (i.e., adult present, but no nest found).

The Grabers and Kirk have incorporated the unpublished records of A. O. Gross and F.

Smith and his students with those of the extensive published record (there are almost 600 references listed in the Literature Cited section). Particularly valuable in this regard is the inclusion of data from transect censuses conducted by A. O. Gross in 1906–1909 and by the Grabers in 1979–1981. Life-history information collected in adjacent states, such as that for the Prairie Warbler (*Dendroica discolor*) in Indiana by V. Nolan, are cited where appropriate in the species accounts.

My only criticism concerns the inclusion of black-and-white photographs or drawings of the warblers and their nests. The photographs add little to the value of the publication. However, as the range maps and figures are of excellent quality and a wealth of information is presented in the text and tables, the inclusion of photographs did not come about at the expense of having to delete more important information. Also, a Table of Contents would have made the species accounts easier to find.

The Grabers and Kirk are to be commended for this addition to their series on the birds of Illinois. Would-be authors of state or regional avifaunal accounts would do well to use this work as a model of how to summarize and present a great deal of information in a clear, accurate, and well-organized manner.—CHARLES F. THOMPSON.

BIRDS OF SOUTHERN CALIFORNIA'S DEEP CANYON. By Wesley W. Weathers. University of California Press, Berkeley, California, 1983:268 pp., 28 color plates, 33 half-tones, 60 line drawings (including figures), 45 tables. $35.00.—This book is the fifth of a series reporting on research conducted at or near the Philip L. Boyd Deep Canyon Research Center of the University of California. The 646 km^2 area which is its subject includes the Deep Canyon region of the Santa Rosa Mountains as well as a portion of the adjacent Coachella Valley (a segment of the Sonoran Desert). The site ranges in elevation from 9 to 2657 m above sea level; a journey from the floor of the Coachella Valley to the top of the Santa Rosa Mountains is thus the ecological equivalent of a latitudinal trip from San Diego to Edmonton, Alberta. Striking habitat changes obviously occur along such an elevational gradient, and the variety of life zones represented sustain a remarkable diversity of bird life: of the 500 bird species known to occur in Southern California, 217 have been recorded in Deep Canyon, and 112 species nest there. Thus, although it is small in area, the Canyon provides a unique opportunity for bird study and a book about its avifauna should be of interest to more than a local readership.

Many of the data on species occurrence and the nesting records presented in the book were collected by the author during 198 days spent censusing (during 684 walks along specific strip transects), photographing or simply observing the birds between March 1977 and December 1980. In addition, many observations recorded by competent birdwatchers since the establishment of the Research Center in 1959 were assembled. As well as adding to the general data base, these provide some insight into the changes in species abundance and/or distribution which have occurred in the area. This and other information on methodology is provided in Chapter 1. Chapter 2 presents a clear and detailed account of the weather and climate of the region. Chapter 3 gives a general overview of the various bird communities found in the area, and includes brief, but useful (particularly for the layman) discussions of the ecological determinants of species diversity, seasonal change, nest density and community structure. In this and the following chapters, energy flow is stressed as being important; the relationship between avian energy requirements and the vegetation characteristic of specific life zones is discussed, including an examination of the effects of birds on the plant life.

Chapters 4 through 12 examine each representative habitat type in more detail. The

vegetation and climate characteristic of the habitats are described, and the results of bird censuses conducted in the zone are presented. The status (migrant, winter or summer visitor, resident) of each species in the habitat is provided as is a general discussion of community structure and, as stated, of energy flow through the habitat. The progression through these chapters is an upward one altitudinally: beginning with the valley floor in Chapter 4, the author takes us on a journey through "Human Habitats," "Alluvial Plain," "Rocky Slopes," "Lower Plateau," "Pinion-Juniper Woodland," "Chaparral," "Coniferous Forest," and finally, the "Streamside" habitat which transects most of this elevational range downwards from the springs and seeps of the upper slopes of surrounding mountains. The chapter on human habitats deals with the types and effects of development that have taken place at the lower elevations of the area. Although some species have probably benefited from increases in the amount of food, water, and nest sites incurred by building homes and golf courses and by planting crops, others have suffered substantially as a result of habitat destruction.

The largest portion of the book (127 out of the total 226 pages) is given over to species accounts. Although all of the 217 species seen in the Canyon are listed in a useful appendix (detailing species occurrences by habitat and month), those which have a significant impact on the ecosystem are emphasized in these accounts. A brief description, including the range, general feeding habits, important behaviors, etc., of each family represented by one or more species breeding in Deep Canyon is provided and each of the 112 nesting species is at least mentioned under the appropriate family heading. In most cases, the descriptions of individual breeding species include average weights for both males and females, taxonomic synonyms for the names used by the author, and the entire geographic range of the species as well as a discussion of its activities in Deep Canyon. I note, as a minor criticism, that the range map for the Gray Vireo (*Vireo vicinior*) (p. 195) is incorrect and in fact, includes only about one-half of the entire breeding and wintering range of the species. A more accurate map is provided by Barlow (p. 86 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation, Keast, A. and E. Morton [eds.]. Smithson. Inst. Press, Washington, D.C. 1980.). One wonders how many of the other maps may be similarly incorrect.

The species accounts, like the habitat descriptions, are concise but filled with valuable information. The author shows considerable skill, in fact, in balancing information useful to the professional ornithologist or ecologist with that interesting to the amateur birdwatcher or naturalist. For the former, substantial amounts of hard scientific data on bird species diversity as well as temporal and habitat distributions are provided; numerous issues for future research are raised, and an extensive bibliography is included. At the same time, the book is eminently readable by the layman. Refreshingly concise discussions of basic ecological concepts and principles are provided and complicated jargon is kept to a minimum; those scientific terms employed are usually clearly defined.

Overall, the book is very readable. While the writing is clear and concise, it contains enough "poetry" to project the author's enthusiasm, respect, and appreciation for the Deep Canyon area. The color and half-tone photographs are superb; they show clear evidence of both skillful photography by the author and careful attention to reproduction by the publisher. In short, "Birds of Southern California's Deep Canyon," is a pleasure to own and despite the limited geographical area covered, should be of interest to both professional and amateur ornithologists all over North America.—Nancy J. Flood.

FOREST IN THE SAND. By Marjory Bartlett Sanger. Atheneum Publishers, New York, 1983: 145 pp. $10.95.—This book is a popular account of the natural history of the scrub forest of Ocala National Forest. The daily life of a Scrub Jay (*Aphelocoma coerulescens*) family is discussed during each season of the year. Interspersed among the jay notes are anecdotal accounts of other species in the area. Most interesting is the description of the origin of words commonly used in the Ocala area and in Florida in general.

The book is clearly fiction and does not present any new scientific information. Unfortunately, some of the natural history reported is questionable. For example, yearling Scrub Jays do not help with nest-building, and breeding female jays do not feed their mates. Also, Sanger puts the water moccasin (*Agkistrodon piscivorus*) into the genus *Natrix,* which is in a different family. A few accounts are possible but seem unlikely, such as a Scrub Jay being eaten by a water moccasin. Considering that these two species occur in different habitats the possibility seems remote. Overall I found the book enjoyable reading in spite of the numerous inaccuracies. Clearly, this book is not a reliable reference of the natural history of the area.—G. THOMAS BANCROFT.

BREEDING BIRDS OF LONG POINT, LAKE ERIE: A STUDY IN COMMUNITY SUCCESSION. 1981. J. D. McCracken, M. S. W. Bradstreet, and G. L. Holroyd. Canadian Wildlife Service Report Series 44. 72 pp. illus. maps. $11.75 in Canada, $14.10 elsewhere.—This is another in the series published by the Canadian Wildlife Service, mainly about the fauna of various parts of Canada. The first part of this report deals with breeding bird censuses including: a general description of the Long Point Peninsula and the vegetational communities found there; the methods used to survey and compare habitats and the census techniques applied; detailed descriptions of the census plots on both the drier dunes, as well as in the extensive marshes; detailed results of the censuses in early, mid, and late successional dune habitats and of three successional stages of marshes. This part concludes with a discussion of succession in bird communities and the overall breeding bird densities on the point.

The second half presents an annotated list of the birds that have or are believed to breed on the Point. Information about abundance, frequency of occurence, population trends, distribution on the Point, habitat preferences, nesting, and egg dates (where known) is presented.

A few errors are corrected on an accompanying sheet. I would like to have seen a few more photographs organized and labelled according to the various successional stages discussed. Although perhaps of little significance to the report, the bird identified as a Great Blue Heron (*Ardea herodias*) on p. 45 would appear to be a Tricolored Heron (*Egretta tricolor*) not normally found there, and the adjacent photo appears to be upside down. Overall, the work provides a very useful example of a study of successional changes in an avian community as well as a compilation of information about the breeding birds of a relatively discrete land area.—R. D. JAMES.

COSTA RICAN NATURAL HISTORY. By Daniel H. Janzen (ed.), Univ. Chicago Press, Chicago, Illinois, 1983:816 pp., 338 figs., 55 tables. $30.00 (paper), $50.00 (cloth).—Janzen has compiled the work of 174 contributors in an ambitious "attempt to write down some of what we already know, in a form that can be quickly digested by the newcomer to Costa Rican field biology." The volume is composed of 11 chapters: Costa Rican field biology,

1400–1980 (11 pp.); biotic history and palaeogeography (23 pp.); climate (12 pp.); geology (16 pp.); soils (3 pp.); agriculture (52 pp.); plants (233 pp.); reptiles and amphibians (75 pp.); mammals (76 pp.); birds (117 pp.); and insects (162 pp.). Some major taxonomic groups (e.g., non-insect invertebrates, fishes) are not covered. Each of the last six chapters has an introductory section and a selected set of species accounts, each with its own bibliography. Many of the species accounts are illustrated with black and white photos. In addition, the last five chapters include checklists of species. The index (27 pp., 4000+ entries) is usefully selective, does not include species names from the checklists, and attributes species accounts "to one or more standard field sites to which they are most relevant." This last feature allows for the easy compilation of a set of species accounts appropriate for individual field sites or regions. This volume is not a field identification guide, but the illustrations will facilitate the identification of selected common or distinctive taxa. The volume's size (paper: 22 × 28 × 3 cm, 1.7 kg) and format exempts it from service as a pocket guide. It is appropriately a reference volume for use at a base. The paper bound edition in my possession is put together well, but is unlikely to survive prolonged field use or careless transportation.

The introduction (29 pp.) and checklist (820+ species) for the chapter on birds were prepared by F. G. Stiles. The introduction focuses on the following topics: avifaunal composition and affinities; zoogeography; avian community structure; seasonal patterns in resources, reproduction, molt, and movement; social systems; and birds in Costa Rican ecosystems. This section, in my view, ranges over an appropriate selection of topics to constitute a balanced and contemporary introduction to avian ecology in Costa Rica. As with introductory sections in the other chapters, the audience that will best be served includes neophytes and experienced students of other taxonomic groups. Experienced readers may find some fault with emphasis or points of omission and detail. A few typographical and editorial errors can be found (e.g., the symbols for humid and dry sites on the Pacific slope are reversed in Fig. 10.3). In the checklist, species are listed by Latin name, without attribution to order or family, and their migratory status is noted. The systematic arrangement and treatment predates that of the 6th edition of the "A.O.U. Check-list." Species abundance, status, and habitat preferences are summarized for each of eight well-studied, geographically diverse locations: La Selva; Osa Peninsula; Palo Verde; Santa Rosa; Las Cruces; Monteverde; Universidad de Costa Rica; and Villa Mills. The 52 species accounts (74 pp.) were contributed by 35 different authors. They are arranged in alphabetical order by Latin name. Except for the presentation of common names in Spanish and English, no consistent internal format or style is followed and the accounts vary somewhat in quality and usefulness. Most accounts are well-written and convey a breadth of natural history information on conspicuous, widespread, or distinctive species of diverse taxonomic affiliation. Overall, the selection of species, apparently done by Janzen, is eclectic and suffers some from the omission of several conspicuous taxa likely to be encountered by many field workers. Notably underrepresented are accipitrids (only the Roadside Hawk [*Buteo magnirostris*]), cotingids (none, *Procnias* and *Tityra* deserve attention), dendrocolaptids (none, family is distinctive though inconspicuous), and the diverse Emberizid fauna. There are no Thraupinae (*Euphonia* spp., Blue–Gray Tanager [*Thraupis episcopus*], Scarlet-rumped Tanager [*Ramphocelus passerinii*] are conspicuous)! Every reader will find several of her or his favorite species covered, but at least one missing; my candidate for inclusion is Blue-and-white Swallow (*Pygochelidon cyanoleuca*). Yet, the omission of several conspicuous and abundant species points out our current, fragmentary knowledge of their biology.

Field biologists working in the Neotropics will find this book an invaluable resource. For the experienced researcher on a taxonomic group, the greatest value may come from the introduction to other taxa and the compilations of general biogeographic information. For

the prospective or inexperienced student of tropical natural history, nowhere else is such an introduction to the region, its organisms, and the directions of recent investigation so accessible. As an educator, I'll use this work as a required text in tropical field courses for advanced undergraduates.

I am impressed and excited by Janzen's book. Conceived and executed as an organic step in the development of tropical biology, it fills the void between field identification guides and keys, on one hand, and advanced specialty texts and primary research literature, on the other. The book offers the beginner an efficient introduction to the exciting middle ground between the overwhelming biotic variety and the daunting conceptual abstraction of tropical ecology. The contributors to this volume deserve commendation for their many labors of love. Once again Dan Janzen has made a major contribution to the study of tropical biology.—William H. Buskirk.

Avian Endocrinology: Environmental and Ecological Perspectives. By Shin-ichi Mikami, Kazutaka Homma, and Masaru Wada (eds.). Japan Scientific Societies Press, Tokyo, Japan; and Springer-Verlag, Berlin, Federal Republic of Germany, 1983:334 pp., numerous black-and-white illustrations, one color plate. $53.00.—The two dozen chapters in this book focus on avian endocrinology from the level of microscopic anatomy to that of the ecosystem. They are grouped into three sections representing increasing levels of organization. The first section, Anatomical and Hormonal Basis for Avian Endocrine Function, concentrates on the structure and function of endocrine organs, especially at the biochemical level. The second section, Environmental Manipulation of Endocrine Function, examines photoperiodism and the role of circadian mechanisms in inducing gonadal growth. The third section, Ecological Aspects of Avian Endocrinology, looks most closely at the annual cycle of reproductive activity.—R.J.R.

Hormones and Behaviour in Higher Vertebrates. By J. Balthazart, E. Pröve, and R. Gilles (eds.). Springer-Verlag, Berlin, Federal Republic of Germany (in the U.S.A. Springer-Verlag New York Inc., New York, New York, 1983:489 pp., 175 black-and-white figures. $55.00.—This book contains the proceedings of a symposium held in West Germany in 1982 under the auspices of the European Society for Comparative Physiology and Biochemistry. Thirty-five chapters are grouped under the following general topics: Brain Mechanisms, Sexual Differentiation, Testosterone Metabolism, Endocrine Cycles, and Bird Behaviour. Fewer than half of the chapters deal specifically with birds, many being concerned with mammals. Major emphasis is on the endocrine aspects of reproductive behavior, its differentiation and activation, courtship and vocal behavior, and care of the young. This work will be of interest both to physiologists and to students of behavior concerned about the mechanisms underlying the development and expression of social and reproductive behavior in birds.—R.J.R.

Care of the Wild. By W. J. Jordan and John Hughes. Rawson Associates, New York, New York, 1983:223 pp., numerous line drawings. $13.95 (cloth), $8.95 (paper).—Subtitled "Family First Aid for All Wild Creatures," this is a guide to providing help for animal victims of accident, poisoning, hunting, or contamination. It is divided into major sections

covering birds, mammals, and other wildlife. The section on birds runs about 80 pages and has chapters on Wildfowl, Other Swimming Birds, Waders, Game Birds, Birds of Prey, Other Birds, and Oil Pollution. Topics covered in each chapter encompass possible handling hazards, approach and capture, transportation, initial care, food, force-feeding, and symptoms, diagnosis, and treatment. Appendices cover Wildlife and the Law, Euthanasia, Composition of Animal Milks, and Wildlife Rehabilitation Centers—United States.—R.J.R.

PHYSIOLOGY AND BIOCHEMISTRY OF THE DOMESTIC FOWL, VOL. 4. By B. M. Freeman (ed.). Academic Press Inc., London, England, 1983:434 pp., numerous black-and-white drawings and photographs. $55.00.—The first three volumes of this series were published more than 10 years ago. Though they remain basic references in avian physiology they have become out of date in many areas because of the progress of research. The present volume is intended to update the original with articles by many of the original authors. The 20 chapters cover topics dealing with food intake, digestive physiology and microflora, respiration, kidney structure and urine formation, metabolism and trace elements, adrenal glands, integument, muscle, erythrocytes and haemoglobins, plasma proteins and kinins, special senses, thermoregulation, and the oviduct.—R.J.R.

CHANGES IN EDITORS

Dr. Keith A. Bildstein will be serving as the Editor of the Wilson Bulletin beginning with Volume 97. As of 15 May 1984, all manuscripts submitted for publication in the journal should be sent to him at the **Department of Biology, Winthrop College, Rock Hill, SC 29733.** All manuscripts received prior to 15 May 1984 will continue to be processed by Dr. Jon C. Barlow.

Dr. George A. Hall has replaced Dr. Robert J. Raikow as Book Review Editor of the Wilson Bulletin. From 1 June 1984 all books for review should be sent to him at the following address: **Dept. Chemistry, P.O. Box 6045, West Virginia University, Morgantown, WV 26506.**

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The Wilson Bulletin

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Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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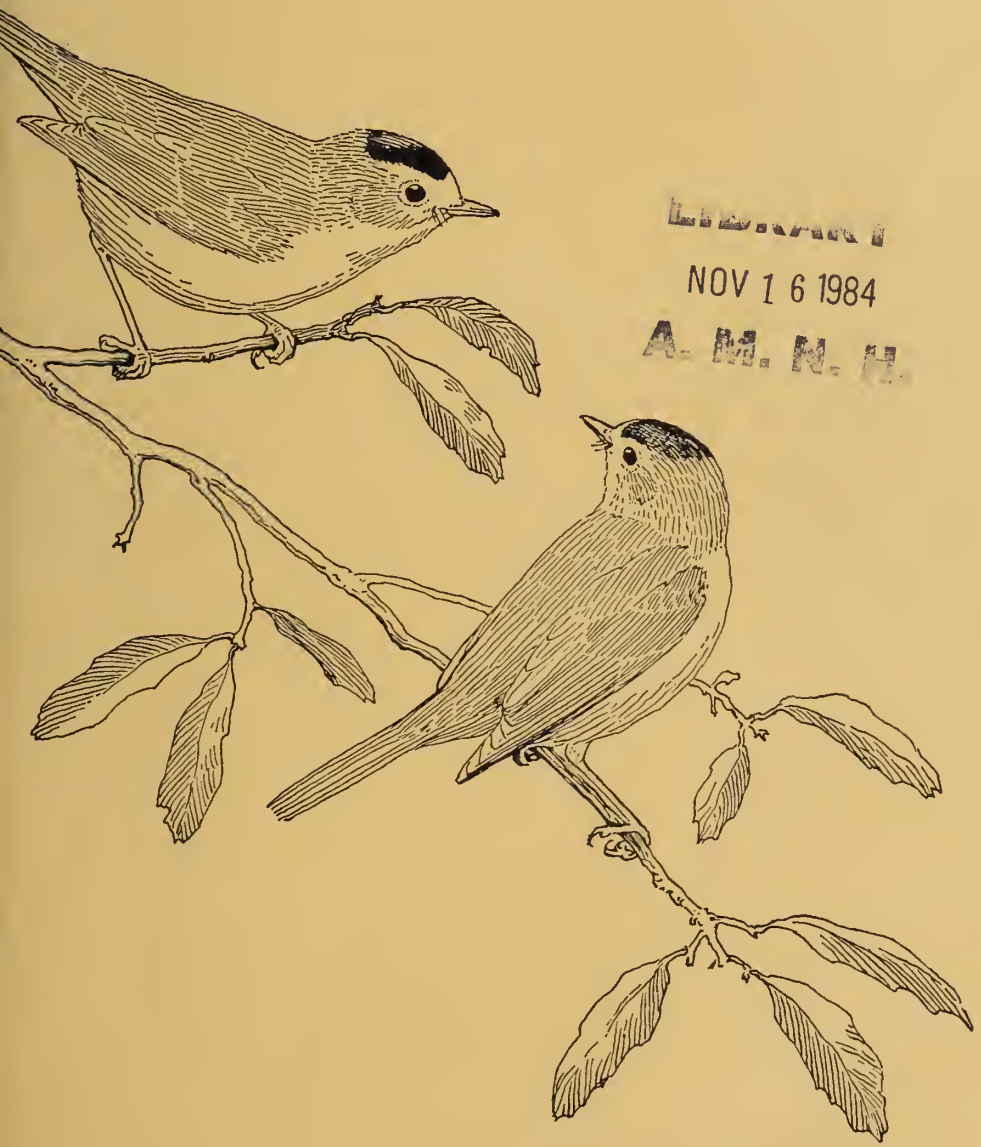

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Chestnut-belted Gnateater (*Conopophaga aurita*), male above and female below.
Painting, in mixed media, by John P. O'Neill.

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A LIST OF BIRDS AND THEIR WEIGHTS FROM SAÜL, FRENCH GUIANA

JAMES A. DICK, W. BRUCE MCGILLIVRAY, AND DAVID J. BROOKS

French Guiana, a department of France, is both the least developed and most sparsely populated of the Guianas and, with the exception of minor perturbations caused by scattered small villages, the avifauna and habitats of the interior parts of the country are little disturbed by human activity. Much of French Guiana is untouched rainforest and the area around Saül (03°37′N, 53°12′W) 175 km SW of Cayenne comprizes many of the tallest forest stands in the country (R. A. A. Oldemann, pers. comm.). Access to the interior is by small boat navigation of rivers and streams or by small planes. Most investigators who have studied the avifauna of the country have worked along the coast or major rivers (Ménégaux 1904, 1907, 1908; Von Berlepsch 1908a, 1908b; Penard and Penard 1908, 1910; Berlioz 1962). In contrast, the Saül site is not near a major river and only Tostain (1980) has reported on birds of the Saül area.

The region in which Saül is located is hilly, largely covered with dense mature rainforests with some land cleared for agriculture. An airstrip 6 km SE of Saül and the road leading to Saül from the NE are bordered by secondary growth forest dominated by trees of the genera *Cecropia, Musa,* and *Artocarpus*. Many introduced fruit (*Citrus* spp., bread fruit [*Artocarpus*], Mango [*Manigtera*], avocado [*Persea*]) and palm (*Arecaceae*) trees grow in the village of Saül. On the outskirts of Saül there is a 400-m^2 area of open grassland formerly used for agriculture, but abandoned for that purpose after the soil nutrients were leached out.

Through the efforts of O.R.S.T.O.M. (Office de la recherche scientifique et technologique d'Outre-mer) foot paths have been cut through local forest in preparation for the establishment of a national park in the area.

Within a few kilometers of Saül the hills are covered with tall trees (40 m) with enormous buttresses. Undergrowth there is very sparse due to the heavy canopy layer and rapid leaching. Our goals were to survey the local avifauna in mid-winter and spring and to obtain weights not previously available for many species.

METHODS

From 23 April to May 1976, J. A. Dick and W. B. McGillivray obtained a reference collection of bird specimens and studied aspects of the natural history and ecology of the avifauna of the Saül area. In 1977, from 21 January–27 February, W. B. McGillivray with D. J. Brooks returned to Saül to continue the fieldwork. The specimens acquired during the first trip are housed in the Royal Ontario Museum (ROM), Toronto, Canada and those of the second trip in the Museum of Natural History, University of Kansas (KU), Lawrence, Kansas.

In 1976, J. A. Dick and W. B. McGillivray set 10, 12-m mist nets in a row in mature rainforest 3 km SE of Saül. The families Apocynaceae, Bursaraceae, Lecythidaceae, Sapotaceae, Leguminosae, Rubiaceae, Anacardiaceae, Moraceae and Arecaceae were conspicuously represented in the rainforest. Most acquisition in 1976, apart from netted birds, was done along the road to the airstrip or near the airstrip itself. In 1977, mist nets were set up in the same area as in 1976. Also in that year, two nets were placed at heights of 10 and 15 m near a flowering *Miconia* tree along the airport road. In addition in 1977, five other nets were positioned along a creek bed in secondary growth 1 km E of the village. Common trees at that site were of the families Euphorbiaceae and Leguminosae.

The rainy season in French Guiana in part encompasses April and May; unstable weather with frequent rain is expected at this time. During the 1976 field season, Saül received an above average amount of precipitation (40 cm in 21 days). January and February are transition months between dry and wet seasons. Nevertheless, prior to our arrival heavy rains fell in 1976 in both of these months.

Mist nets were checked at least four times a day from 07:30 to 17:30. After the final daily visit at 17:30 the nets were furled to prevent damage at night by bats. The nets were opened the next morning 1 h prior to the first net check at 07:30. Between net checks one or two sorties searching for birds were made per day that covered from 3–6 km from the main net set.

We follow the nomenclature of Morony et al. (1975) for species and Peters et al. (1934–1979) for the subspecies.

SPECIES ACCOUNTS AND COMMENTS

Great Tinamou (*Tinamus major*).—Downy young male (ROM 125756) 71 g, 16 May 1976; adult male (KU 72056) 970 g, 23 January 1977. *T. major* was not common near Saül, probably due to hunting pressures, although birds of the genus *Crypturellus* were heard frequently in the dense forest some distance from the village.

Variegated Tinamou (*Crypturellus variegatus*).—Immature male (ROM 125757) 250 g, 15 May 1976. This was a common species locally.

Rufescent Tiger-Heron (*Tigrisoma lineatum*).—Adult female (KU 72054) 965 g, 26 January 1977. Presence of this species was noteworthy because of the low level of water in the small creek along which the bird was taken during this dry season.

Swallow-tailed Kite (*Elanoides forficatus*).—We saw several individuals of this species

foraging on insects just above the canopy, 24 April, 2 and 13 May 1976 (see also McGillivray and Brooks 1979).

Double-toothed Kite (*Harpagus bidentatus*).—Adult male (KU 72071) 170 g, donated to the field crew 26 January 1977. The stomach of this bird contained insect remains.

Plumbeous Kite (*Ictinia plumbea*).—We observed this bird foraging above the canopy, 2 May 1976.

White Hawk (*Leucopternis albicollis*).—A single individual was seen perched 40 m up in a tree near the village, 25 April 1976.

Harpy Eagle (*Harpia harpyja*).—McGillivray noted seeing this species on 24 April 1976. An adult female (KU 71976) was found dead and was donated to the field crew by locals, 23 January 1977.

Red-throated Caracara (*Daptrius americanus*).—Flocks of up to 20 individuals were seen on 13 and 14 May 1976 in local mature forest.

Little Chachalaca (*Ortalis motmot*).—Adult female (KU 72021) 500 g, in breeding condition, 22 January 1977. This species was heard calling in thick secondary growth bordering the airstrip, 26 April 1976. The specimen was obtained at this site in 1977. Haverschmidt (1968) noted that it is usually found in the coastal or savanna areas in Surinam.

Marail Guan (*Penelope marail*).—Immature male (ROM 25758) 920 g, 12 May 1976; adult female (ROM 125760) 800 g, 15 May 1976; adult female (ROM 125759) 1000 g; adult male (KU 72081) 930 g, 29 January 1977. The specimens were obtained in mature forest. The adults had ova 2 and 3 mm in diameter, respectively.

Gray-winged Trumpeter (*Psophia crepitans*).—Adult male (KU 72080) 1050 g, with gonads enlarged, 20 February 1977. The *woo-woo-woo* call of this species is easily imitated by local hunters and used to attract birds for easy capture by them.

Solitary Sandpiper (*Tringa solitaria*).—Adult male (KU 72050) 40 g, 24 February 1977. Although Haverschmidt (1968) commented that *Tringa* winters inland, it was surprising to find a pair, from which our specimen came, wintering in a tiny clearing surrounded by thick forest.

Ruddy Ground-Dove (*Columbina talpacoti*).—Two adult males (KU 71851, KU 72066) 45 g, 50 g, 22 and 28 January 1977. This common species was found in open burns and open wet grassland.

Gray-fronted Dove (*Leptotila rufaxilla*).—Adult females (ROM 125761, ROM 126590) 175 g, 180 g, in breeding condition, 20 April and 15 May 1976. Adult female (KU 71826) 170 g, in breeding condition, 13 February 1977. This species was common in dense secondary growth.

Red-and-green Macaw (*Ara chloroptera*).—Adult male (KU 71831) 1250 g, donated to the field crew 30 January 1977. Tostain (1980) indicated that this species is new to Saül; however, de Schauensee and Phelps (1978) included the Guianas within the distribution of this species.

White-eyed Parakeet (*Aratinga leucophthalmus*).—Previously McGillivray positively identified individuals of this species, 24 April 1976. Three adult females (KU 71952, KU 71883, and KU 71531) 100 g, 140 g, and 155 g, 12, 14, and 16 February 1979; adult male (KU 71899) 154 g, 12 February 1977. Haverschmidt (1968) commented that *A. leucophthalmus* is not well known from the interior of Surinam.

Painted Parakeet (*Pyrrhura picta*).—Three adult males (KU 71804, KU 71925, KU 71926) 66 g, 67 g, and 65 g, 24 and 28 January 1977.

Blue-headed Parrot (*Pionus menstruus*).—Five adult males (KU 71939, KU 71940, KU 72082, KU 72034, KU 72039) $\bar{x} = 250 \pm 4.5$ g (242–254 g), in breeding condition, 28 January (2), 6 February (2), 8 February (1) 1977; adult female (KU 71940) 263 g, in breeding condition, 28 January 1977.

Dusky Parrot (*P. fuscus*).—Adult female (KU 71543) 198 g, with ovary enlarged, 5 February 1977.

Red-fan Parrot (*Deroptyus accipitrinus*).—Five individuals of this species were observed 25 April 1976 north of the airstrip. One bird was perched on a branch 10 m from the ground over the path and displayed its fan and vocalized in our presence.

Squirrel Cuckoo (*Piaya cayana*).—Two adult males (ROM 125762, ROM 126632) 100 g, 110 g, 2 and 8 May 1976; two adult males (KU 71859, KU 71521) 106 g, 112 g, 25 January and 5 February; three adult females (KU 71520, KU 71874, KU 72068) 108 g, 104 g, and 100 g, 25 January, 5 and 8 February 1977.

Smooth-billed Ani (*Crotophaga ani*).—Adult male (KU 72051) 106 g, in breeding condition, 21 February 1977. A small flock was seen at the Saül airstrip on 24 April 1976.

Spectacled Owl (*Pulsatrix perspicillata*).—Adult female (KU 72052) 850 g, found dead in grassland near Saül, 3 February 1977.

Lesser Nighthawk (*Chordeiles acutipennis*).—Adult female (KU 72063) 60 g, 6 February 1977, from the Saül airstrip. Usually found in savannas in Surinam (Haverschmidt 1968).

Blackish Nightjar (*Caprimulgus nigrescens*).—Adult male (ROM 125763) 35 g, 25 April 1976. This bird was flushed from the ground at the Saül airstrip, the only site where this species was encountered.

Band-rumped Swift (*Chaetura spinicauda*).—Three males (ROM 125766, ROM 125767, ROM 125768) 15.2 g, 15 g and 13.8 g, and three females (ROM 125764, ROM 125765, ROM 127634) 16 g, 17 g, and 14.5 g, 25 April 1976. These specimens were all taken from a flock of over 100 birds as they foraged 20 m off the ground over the airstrip.

Rufous-breasted Hermit (*Glaucis hirsuta*).—Two males (ROM 125770, ROM 127639) 7.5 g, 6.8 g, 9 and 15 May; female (ROM 125769) 6.5 g, 7 May 1976; adult female (KU 71855) 6.5 g, 27 January 1977.

Long-tailed Hermit (*Phaethornis superciliosus*).—Adult male (ROM 126771) 5 g, 27 April 1976; two females (ROM 125773, ROM 127636) 3.5 g, 3.5 g, 28 April and 12 May 1976; two adult males (KU 71860, KU 72040) 4 g, 5 g, 28 January and 11 February; one unsexed adult (KU 73383) 4 g, 31 January; adult female (KU 71924) 4 g, 22 January 1977. This species was abundant near Saül, being encountered daily.

Great-billed Hermit (*P. malaris*).—Two adult males (ROM 125772, ROM 127654) 10 g, 7.5 g, 26 April and 12 May 1976.

Gray-breasted Sabrewing (*Campylopterus largipennis*).—One male (ROM 125776) 9.5 g, 5 May and a female (ROM 125777) 8 g, 6 May 1976; adult male (KU 71829) 9 g, 14 February; two adult females (KU 71811, KU 72047) 7.5 g, 8 g, 4 and 13 February 1977. Birds were encountered in edge habitat along the airstrip road. This species is uncommon in adjacent Surinam (Haverschmidt 1968).

Blue-chinned Sapphire (*Chlorestes notatus*).—Two adult females (KU 71827, KU 71902) 4 g, 4.5 g, 11 and 20 February 1977.

Fork-tailed Woodnymph (*Thalurania furcata*).—Adult male (ROM 125778) 4 g, 14 May 1976; adult male (KU 71828) 5 g, 12 February; unsexed adult (KU 73385) 4 g, 18 February; adult female (KU 71838) 4 g, 1 February 1977.

Black-eared Fairy (*Heliothrix aurita*).—Male (ROM 125774) 5 g, 16 May; female (ROM 125775) 5 g, 7 May 1976; adult male (KU 71534) 5 g, 17 February 1977. Another edge species, Haverschmidt (1968) considered it rare in hilly forests in the interior of Surinam.

Black-tailed Trogon (*Trogon melanurus*).—Unsexed adult (KU 73311) 52 g, 29 January; adult female (KU 71537) 56 g, 2 February 1977. White-tailed Trogon (*T. viridis*).—Adult male (KU 71816) 96 g, 25 January 1977.

Black-throated Trogon (*T. rufus*).—Unsexed adult (KU 73311) 52 g, 29 January 1977; adult female (KU 71537) 56 g, 2 February 1977.

Violaceous Trogon (*T. violaceus*).—Adult female (ROM 125779) 53.5 g, 7 May 1976; adult male (KU 71867) 51 g, 21 January 1977. This species was fairly common in the Saül area in 1976.

Blue-crowned Motmot (*Momotus momota*).—Adult male (ROM 126646) 120 g, 13 May 1976; adult male (KU 72017), adult female (KU 71533) 142 g, 138 g, 16 and 17 February 1977. This species was seemingly uncommon near Saül.

Yellow-billed Jacamar (*Galbula albirostris*).—Male (ROM 125786) 19 g, 19 May 1976; female (ROM 127662) 20 g, 11 May 1976; adult male (KU 72026) 18 g, 17 February; two adult females (KU 72042, KU 72043) 20 g, 19 g, 9 and 17 February 1977. This species and *G. dea* were frequently seen flycatching from dead branches in open areas or lower canopy of the forest.

Paradise Jacamar (*G. dea*).—Two adult males (ROM 125784, ROM 125785) 31 g, 31.5 g, 2 May 1976; adult male (KU 71891) 25 g, and an unsexed adult (KU 73310) 29 g, 29 January; two adult females (KU 71853, KU 71890) 30 g, 23 g, 22 and 29 January 1977.

Great Jacamar (*Jacamerops aurea*).—Adult female (KU 71856) 66 g, 27 January 1977.

White-necked Puffbird (*Notharchus macrocrhynchus*).—Adult female (KU 71522) 85 g, 3 February 1977. An adult was seen on 24 April 1976 while perched on a dead branch at the outer edge of a tree crown about 30 m above the forest floor.

Spotted Puffbird (*Bucco tamatia*).—Adult male (KU 71871) 38 g, 2 February 1977.

White-chested Puffbird (*Malacoptila fusca*).—Female (ROM 125782) 39 g, 6 May 1976. Apparently this species is not common in Surinam (Haverschmidt 1968).

Black Nunbird (*Monasa atra*).—Female (ROM 125781) 1 May 1976; two adult males (KU 71806, KU 71861) 94 g, 104 g, 22 and 28 January; three adult females (KU 71934, KU 72053, KU 71862) 84–97 g, 26 and 28 January 1977.

Black-spotted Barbet (*Capito niger*).—Adult male (ROM 125780) 56 g, 2 May; adult female (ROM 127644) 57.5 g, with an enlarged oviduct, 15 May 1976; adult male (KU 71529) 58 g, and an adult female (KU 71519) 60 g, 5 February 1977.

Green Aracari (*Pteroglossus viridis*).—Two adult males (KU 71870, KU 71869) 136 g, 156 g, 3 February 1977.

Black-necked Aracari (*P. aracari atricollis*).—This species was observed foraging about 30 m above the ground on a green fig-type fruit on 3 May 1976.

Guianan Toucanet (*Selenidera culik*).—Male (ROM 125788) 140 g, 14 May 1976; adult male (KU 72015) 140 g, 24 January 1977.

Red-billed Toucan (*Ramphastos tucanus*).—Adult female (ROM 125787) 600 g, 27 April 1976; adult female (KU 71957) 560 g, in breeding condition, 7 February 1977. This species seemed to be more solitary in its habits than other toucans seen.

Yellow-tufted Woodpecker (*Melanerpes cruentatus*).—Two adult males (KU 72019, KU 72024) 63 g, 58 g, 16 February; adult female (KU 71553) 62 g, 7 February 1977. In January 1977, a large family group used a nest cavity 25 m above the ground.

Yellow-throated Woodpecker (*Piculus flavigula*).—Male (ROM 125790) 60 g, 11 May; female (ROM 125789) 15 May 1976; adult female (KU 71854) 56 g, 26 January 1977. Both birds from 1976 were foraging on tree trunks from 7–12 m above the ground.

Chestnut Woodpecker (*Celeus elegans*).—Adult male (KU 72014) 176 g, in breeding condition, 24 January 1977.

Lineated Woodpecker (*Dryocopus lineatus*).—Male (ROM 125794) 200 g, 20 April 1976; adult female (KU 71922) 209 g, 22 January 1977. This species was normally seen on tree trunks far above the forest floor.

Red-necked Woodpecker (*Phloeoceastes rubicollis*).—Adult male (ROM 125792) 230 g, 4 May; two females (ROM 125793, ROM 125791), an immature and an adult, 182 g, 200 g, 16 and 10 May 1976, respectively; two adult males (KU 71886, KU 72058) 220 g, 239

g, 23 January and 12 February 1977. Often seen within 2 m of the ground foraging for insects on tree trunks, this species was the most common of the woodpeckers seen in 1977.

Plain-brown Woodcreeper (*Dendrocincla fuliginosa*).—Adult female (ROM 125799) 39 g, 10 May 1976. This species was fairly common in mature forest.

White-chinned Woodcreeper (*D. merula*).—Adult female (ROM 125800) 44 g, 29 April 1976. Our specimen came from edge near mature forest. Haverschmidt (1968) considered this species uncommon in Surinam.

Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*).—Two adult males (ROM 126861, ROM 127209) 4 and 14 May 1976; two males with skulls not ossified (ROM 125801, ROM 127207) 28 April and 14 May; one adult female (ROM 127658) 13 g, 9 May 1976; two adult males (KU 71842, KU 71884) with gonads enlarging, 31 January and 1 February; two adult females (KU 71839, KU 71840) both 13 g, 31 January 1977. The eight males weighed from 13–14 g. This species was common and tended to forage within 3 m of the forest floor on tree trunks and often was caught in the bottom bay of a mist net.

Barred Woodcreeper (*Dendrocolaptes certhia*).—Adult male (KU 71845), adult female (KU 71837) 70 g, 69 g, 29 January 1977.

Chestnut-rumped Woodcreeper (*Xiphorhynchus pardalotus*).—Adult male (ROM 125797), adult female (ROM 125796) 36.8 g, 33 g, 4 and 5 May 1976; adult male (KU 72075) 40 g, 17 February, two adult females (KU 71893, KU 71855) 35 g, 37 g, 29 January and 17 February 1977.

Buff-throated Woodcreeper (*X. guttatus polystictus*).—Adult female (ROM 125795) 59.5 g, with ovary enlarged, 30 April 1976; three adult males (KU 71866, KU 21936, KU 71542) 66 g, 68 g, and 74 g, with gonads enlarged, 23, 25 January and 5 February 1977. Haverschmidt (1968) recorded this species from the coastal mangroves and sand ridges of Surinam.

Curve-billed Scythebill (*Campylorhamphus procurvoides*).—Adult male (ROM 125798) 33 g, with gonads enlarged, 29 April 1976. Apparently it is rare in Surinam (Haverschmidt 1968).

Plain-crowned Spinetail (*Synallaxis gujanensis*).—Two adult females (KU 71539, KU 72043) 20.5 g, 18 g, 3 and 5 February 1977. This species was seen by us foraging in the village nearly every day. McGillivray in his journal noted its call as a loud *ke-he* and he further noted how commonly the call was heard in the village. We found an occupied nest of this species 8 May in an abandoned termite nest.

Cabinis' Spinetail (*S. cabanisi obscurior*).—Adult male (no number) 20 g, an unsexed adult (KU 73386) 19 g, and an adult female (KU 71901) 18.5 g, 9, 2, and 6 February 1977, respectively.

Rufous-tailed Foliage-gleaner (*Philydor ruficaudatus*).—Two adult males (ROM 125808, ROM 125809) 28 g, 24 g, 4 May and 28 April; female (ROM 125810) 25 g, 4 May 1976.

Rufous-rumped Foliage-gleaner (*P. erythrocercus*).—Two adult males (KU 71526, KU 71557) 25.5 g, 35 g, adult female (KU 71846) 24 g, 5, 6 February and 29 January 1977.

Olive-backed Foliage-gleaner (*Automolus infuscatus cervicalis*).—Adult male (ROM 125803) 33.5 g, adult female (ROM 125806) 35 g, with ovary enlarged, 4 May and 28 April 1976, respectively; immature male (ROM 125804) 32 g, immature female (ROM 127648) 30 g, 5 and 13 May 1976, respectively; two adult males (KU 71876, KU 72079) both 32 g, with gonads enlarged; adult female (KU 71844) 35 g, with largest ovum = 13 × 12 mm, 21 February 1977.

Ruddy Foliage-gleaner (*A. rubiginosus obscurus*).—Adult male (ROM 125807) 32 g, 5 May 1976.

Chestnut-crowned Foliage-gleaner (*A. rufipileatus consobrinus*).—Adult male (KU 71878) 35 g, with testes enlarged, 29 January 1977.

Short-billed Leafscraper (*Sclerurus rufigularis fulvigularis*).—Adult female (ROM 125811)

20.8 g, 4 May 1976; adult male (KU 71535) 22 g, with gonads enlarged, adult female (KU 71806) 22 g, 3 and 4 February 1977.

Plain Xenops (*Xenops minutus ruficaudus*).—Adult male (ROM 125805) 13.8 g, adult female (ROM 125802) 11.5 g, 26 and 20 April 1976.

Fasciated Antshrike (*Cymbilaimus lineatus*).—Adult female (ROM 125812) 37 g, 2 May 1976. This bird was in a mixed flock foraging in the canopy about 10 m above the ground.

Mouse-colored Antshrike (*Thamnophilus murinus*).—Two adult males (ROM 125834, ROM 125835) 19 g, 21 g, 2 and 5 May 1976. Four adult males (KU 71914, KU 71942, KU 71943, KU 71949) $\bar{x} = 17.6 \pm 0.37$ g (17–18 g), 31 January, 19 and 20 February 1977.

Dusky-throated Antshrike (*Thamnomanes ardesiacus*).—Two specimens, one an adult male (no number) and another bird, sex unknown (no number) 31 January 1977 and 20 February 1977, respectively.

Cinereous Antshrike (*T. caesius glaucus*).—Three adult females (ROM 125829, ROM 125830, ROM 127656) 2, 4, and 13 May 1976; four males (ROM 125826, ROM 125827, ROM 125828, ROM 127666) 5, 4, 11, and 14 May, respectively; three adult males (KU 71913, KU 71538, KU 72074) 31 January, 4 and 17 February; two adult females (KU 71834, KU 71822) 2 and 3 February 1977. The seven adult males' average weight was 16.3 ± 1.4 g (13–17.5 g), and the five adult females' weight averaged 15.6 ± 1.3 g (15–18 g). This species was often represented in the flocks that foraged in the forest canopy.

Brown-bellied Antwren (*Myrmotherula gutturalis*).—Immature female (ROM 125847) 4 May 1976; adult male (KU 71907) 9 g, 17 February 1977; three adult females (KU 71850, KU 71813, KU 72073) 31 January, 4 and 17 February 1977. The four females' average weight was 9.1 ± 0.2 g (9–9.5 g).

White-flanked Antwren (*M. axillaris*).—Three adult males (ROM 125848, ROM 125849, ROM 125850) 12, 4, and 8 May 1976, respectively. Two adult males (KU 71843, KU 71900) both birds with gonads enlarged, 31 January and 7 February 1977. The average weight for the five adult males was 7.5 ± 0.7 g (7–9 g).

Long-winged Antwren (*M. longipennis*).—Three adult males (ROM 125842, ROM 125843, ROM 125844) 14 and (latter 2) 4 May 1976, respectively; two adult females (ROM 125846, ROM 127640) 4 and 6 May 1976, immature female (ROM 125845) 4 May 1976; adult male (KU 71912) with testis = 7 × 3 mm, 31 January 1977; two other adult males (KU 71915, KU 71903) 31 January and 17 February 1977; two adult females (KU 71916, KU 71906) 1 and 17 February 1977. The six adult males' average weight was 8.9 ± 1.8 g (8–13 g) and the average weight for the five females was 8.8 ± 1 g (7.5–10 g).

Gray Antwren (*M. menetriesii cinereiventris*).—Three adult males (ROM 125851, ROM 125852, ROM 127663) 8.5 g, 8.7 g, and 9 g, 4 and 6 May 1976; adult female (ROM 125853) 9.5 g, 4 May 1976; adult female (KU 71905) 8.5 g, 17 February 1977.

Dot-winged Antwren (*Microrhopias quixensis microsticta*).—Adult male (ROM 125854) 9.5 g, 7 May 1976; adult female (ROM 125855) 10 g, 13 May 1976; adult male (KU 71812) 9 g, 3 February 1977. This species was observed in May 1976 in mixed flocks foraging in dense secondary growth usually within 2 m of the forest floor.

Dusky Antbird (*Cercomacra tyrannina saturator*).—Immature female (ROM 127633) 15 g, 12 May 1976.

White-browed Antbird (*Myrmoborus leucophrys angustirostris*).—Adult male (ROM 125837) 20 g, 12 May 1976; two adult males (KU 71889, KU 71880) 22 g, 20 g, 29 January 1977; three adult females (KU 72064, KU 71919, KU 71917) 22 g, 20 g, and 19 g, 27, 30 and 31 January 1977.

Warbling Antbird (*Hypocnemis cantator*).—Adult male (ROM 125856) 13 g, 7 May 1976; adult female (ROM 127638) 12 g, 12 May 1976.

Black-headed Antbird (*Percnostola rufifrons*).—Two adult males (ROM 125824, ROM

125825) 28 April and 10 May 1976; immature male (ROM 125823) 9 May 1976; adult male (KU 71911) 8 February 1977. These four males weighed 30.4 ± 1.8 g (28.3–33 g).

Ferruginous-backed Antbird (*Myrmeciza ferruginea*).—Adult male (ROM 125836) 29 g, 5 May 1976; two adult males (KU 71524, KU 71525) 27 g, 26 g, 20 and 21 February 1977.

Black-throated Antbird (*M. atrothorax*).—Adult male (KU 71888) 15 g, 29 January 1977.

White-plumed Antbird (*Pithys albifrons*).—Adult male (ROM 125814) 21 g, 12 May; three adult females (ROM 125813, ROM 125815, ROM 125816) 30 April, 6 and 12 May 1976; adult male (KU 71551) 21 g, testis = 7 × 3 mm, 5 February 1977; adult female (KU 71552) largest ovum = 6 × 4 mm, 5 February 1977; three adult females (KU 71832, KU 72028, KU 71547) 1, 17, and 20 February 1977; adult male (KU 71546) 20 g, 20 February 1977. These seven adult females weighed an average of 22.2 ± 1.4 g (20–24.5 g). This species was observed in small flocks following an army ant column north of the airstrip on 25 April 1976.

Rufous-throated Antbird (*Gymnopithys rufigula*).—Adult male (ROM 125818) with testis = 6 × 3 mm, adult female (ROM 125817) both 27 April 1976; three adult males (KU 72076, KU 71548, KU 71824) 18, 19, and 21 February 1977; adult female (KU 71536) 29.5 g, 4 February 1977. The male (KU 72076) had an enlarged testis measuring 8 × 4 mm. The four males' average wieght was 28 ± 1.9 g (25–31 g).

Scale-backed Antbird (*Hylophylax poecilonota*).—Adult male (ROM 125839) 17.5 g, gonads enlarged; adult male (ROM 125838) 28 April and 16 May 1976; three adult females (ROM 125840, ROM 125841, ROM 127661) 12, 1 and 10 May 1976, respectively; adult male (KU 71544) 17 g, female (KU 71946) 17 g, 20 February 1977. The four females' average weight was 16.9 ± 0.6 g (16–17.8 g). Haverschmidt (1968) considered this species to be rare in the Savanna forests in Surinam.

Rufous-capped Antthrush (*Formicarius colma*).—Adult male (KU 71545) 44 g, with testis = 10 × 7 mm, 19 February 1977. This species is rare in Surinam (Haverschmidt 1968).

Black-faced Antthrush (*F. analis crissalis*).—Immature male (ROM 125831) 66 g, 10 May 1976.

Spotted Antpitta (*Hylopezus macularius*).—Adult male (ROM 125857) 38 g, 6 May 1976; adult male (KU 71949) 43 g, 19 February 1977.

Chestnut-belted Gnateater (*Conopophaga aurita*) (Frontispiece).—Adult male (ROM 125858) 13.2 g, 5 May 1976; adult female (ROM 125859) 12 g, 11 May 1976. Both birds had enlarged gonads.

Ringed Antpipit (*Corythopis torquata anthoides*).—Adult female (KU 71945) 15 g, 19 February 1977.

Screaming Piha (*Lipaugus vociferans*).—Three adult males (KU 71920, KU 72057, KU 71951), all three with testes larger than 10 × 5 mm and body weights of 65–82 g, 23 January and 11 February 1977. This bird's call is a loud shrill *pee-yee-pee-ooo* that seems to originate much higher in the canopy than its actual source.

Black-tailed Tityra (*Tityra cayana*).—Two adult males (KU 72055, KU 71858) weighing 64 g and 62 g, were obtained 22 and 25 January 1977. An active nest of this species was noted 31 January 1977. It was located 33 m above the forest floor in the end of a hollow branch.

Spangled Cotinga (*Cotinga cayana*).—Juvenile male (no number) 65 g, 21 January 1977; adult female (KU 71923) 73 g, 26 January 1977.

Purple-throated Fruitcrow (*Querula purpurata*).—Two adult males (ROM 125861, ROM 125862) 8 May 1976; two adult males (KU 71927, KU 71810) 28 January and 3 February 1977; adult female (KU 72020) 88 g, 24 January 1977. The four males' average weight was

107.5 ± 8.9 g (100–122 g). This species was frequently seen in tiered, swampy rainforest usually more than 6 m above the forest floor.

Capuchinbird (*Perissocephalus tricolor*).—Adult male (ROM 125860) 360 g, 11 May 1976. McGillivray noted that the call is reminiscent of a chain saw. He also comments that the species is eaten by local people.

Golden-headed Manakin (*Pipra erythrocephala*).—Three adult males (ROM 125874, ROM 125875, ROM 125876) 5 May, 29 April and 6 May, respectively; two adult females (ROM 125878, ROM 127651) 5 and 12 May 1976; sub-adult male (KU 71929) with some orange feathers appearing as flecks on the crown, 30 January 1977; one adult female (KU 72049) with the largest ovum = 6 × 5 mm, 2 February; three adult females (KU 71928, KU 71930, KU 71819) 29, 31 January and 6 February 1977. The four males' average weight was 10.8 ± 1.1 g (9.5–12.5 g) and the six females weighed an average of 12.5 ± 1.5 g (11.8–14.5 g).

White-crowned Manakin (*P. pipra*).—Two adult males (ROM 125871, ROM 125872) 29 April and 16 May 1976; immature male (ROM 125873) 30 April 1976; adult female (ROM 125877), immature female (ROM 127636) 29 April and 16 May 1976; adult male (KU 71530) testis = 6 × 3 mm, 4 February 1977; two females (KU 72081, KU 71857) with largest ova = 4 × 4 mm and 2 × 2 mm, 16 and 20 February 1977, respectively. The average weight for the four males was 11.2 ± 0.9 g (10.2–12.5 g) and the four females weighed an average of 13.1 ± 0.7 g (12.4–14 g).

White-fronted Manakin (*P. serena*).—Four adult males (ROM 125866, ROM 125867, ROM 125868, ROM 125869) 5 and 8 May 1976; adult male (ROM 125970) 29 April 1976; immature male (ROM 127657) 10 May 1976; two adult males (no number, KU 71938) 31 January and 1 February 1977; juvenile male (KU 71833) 2 February 1977; adult female (KU 72048) 11 g, 31 January 1977. The nine males' average weight was 11.4 ± 0.4 g (10.8–12 g).

White-bearded Manakin (*Manacus manacus*).—Two immature males (ROM 126759, ROM 127649) 13 and 15 May 1976; adult male (KU 71807) testis = 6 × 3 mm, 2 February 1977; two adult females (KU 71879, KU 71540) with largest ova = 2 × 2 mm and 4 × 4 mm, 29 January and 3 February 1977; two adult females (KU 71849, KU 71809) 29 January and 2 February 1977. The five males' average weight was 17 ± 2 g (14–20 g) and the four adult females weighed an average of 15.5 ± 3 g (12–20 g).

Tiny Tyrant-Manakin (*Tyranneutes virescens*).—Female (ROM 127643) 11 g, 4 May 1976. This bird was taken at the edge of the mature forest. De Schauensee (1970) did not include French Guiana in the range of this species and thus our specimen constitutes the first record of this species for French Guiana.

Wing-barred Manakin (*Piprites chloris chlorion*).—Immature male (ROM 125865) 16.5 g, 2 May 1976.

Thrush-like Manakin (*Schiffornis turdinus wallacii*).—Two adult males (ROM 125880, ROM 127664) 32 g, 30 g, 13 and 15 May 1976; two adult males (KU 71877, KU 71904) 30.4 g, 30 g, 1 and 18 February 1977.

Long-tailed Tyrant (*Colonia colonus poecilonotus*).—This species was fairly common near Saül, but no specimens were acquired. This species was often observed flycatching from a dead branch. McGillivray noted on 8 May 1976 that a bird perched on an exposed stump 30–40 m high and uttered its call between foraging sorties. Ten foraging sorties were observed in which the bird caught insects within 5 m of the perch, returning to the same perch after each catch.

Fork-tailed Flycatcher (*Tyrannus savana*).—An individual of this species was seen by McGillivray in the open area near the Saül airstrip on 25 April 1976.

Tropical Kingbird (*Tyrannus melancholicus*).—Adult female (ROM 127208) 40.8 g, 7 May 1976. This bird was found in open scrub habitat near the Saül airstrip.

Variegated Flycatcher (*Empidonomus varius rufinus*).—Adult male (ROM 125883) 26 g, 15 May 1976.

Piratic Flycatcher (*Legatus leucophaius*).—One bird was identified on 24 April 1976 in the edge habitat near the Saül airstrip.

White-ringed Flycatcher (*Conopias parva*).—Adult male (KU 72062) 24 g, 10 February 1977.

Boat-billed Flycatcher (*Megarhynchus pitangua*).—Adult female (KU 71913) 60 g, 31 January 1977.

White-crested Spadebill (*Platyrinchus platyrhynchos*).—Adult male (ROM 125882) 13 g, adult female (ROM 125881) 12.8 g, 28 April 1976; adult female (KU 71835) 12 g, 1 February 1977. This species was occasionally seen foraging within 1 m of the forest floor.

Yellow-margined Flycatcher (*Tolmomyias assimilis examinatus*).—Adult male (KU 71954) 12.5 g, 1 February 1977; adult female (KU 71918) 12 g, 6 February 1977. An individual of this species was seen by McGillivray on 1 May 1976.

Gray-crowned Flycatcher (*T. poliocephalus sclateri*).—Immature female (ROM 125890) 12 g, 26 April 1976.

Rusty-margined Flycatcher (*Myiozetes cayanensis*).—This species was seen in the old field habitat bordering the Saül airstrip, 24 April 1976. Two adult males (KU 72067, no number) 25 g, 28 g, the latter with testes = 15 × 5 mm, 18 and 21 February 1977.

Great Kiskadee (*Pitangus sulphuratus*).—Between 23 April and 17 May 1976, this species was regularly heard and seen in Saül and in the old field habitat by the airstrip.

Bright-rumped Attila (*Attila spadiceus*).—Adult female (ROM 127653) 38 g, 11 May 1976; adult female (KU 71815) 35 g, 3 February 1977.

Grayish Mourner (*Rhytipterna simplex fredeici*).—Two adult males (ROM 125864, ROM 127655) 1 and 15 May 1976; two adult males (KU 72069, KU 71541) 25 January and 5 February 1979; adult female (KU 71808) 36 g, 3 February 1977. The four adult males' average weight was 35.7 ± 1.8 g (33–38 g).

Cinereous Mourner (*Laniocera hypopyrrha*).—Adult female (ROM 125863) 47.7 g, 5 May 1976. This and the above species were seen foraging together in the canopy.

Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*).—Adult male (ROM 125893) 7.5 g, 26 April 1976. This species seemed to prefer the lower strata of the forest.

Sulphur-rumped Flycatcher (*Myiobius barbatus*).—Three adult males (ROM 125888, ROM 125889, ROM 127646) 28 April (first two) and 10 May 1976; two adult males (KU 71848, KU 71554) 30 January and 8 February 1977. The average weight of the five adult males was 11.3 ± 1.2 g (9.3–12.5 g).

Royal Flycatcher (*Onychorhynchus coronatus*).—Two adult males (ROM 125886, ROM 125887) both 14 g, 4 and 15 May 1976. The distraction display of this species has been described elsewhere (Dick and Mitchell 1979).

Rufous-tailed Flatbill (*Ramphotrigon ruficauda*).—Adult male (ROM 125882) 19 g, 4 May 1976.

Common Tody-Flycatcher (*Todirostrum cinereum*).—Adult female (KU 72072) 6.5 g, with ovary enlarged (7 × 3 mm), 17 February 1977.

White-eyed Tody-Tyrant (*Idioptilon zosterops*).—Adult male (ROM 127642) 10.5 g, 10 May 1976; adult female (KU 71523) 8 g, 20 February 1977.

Olive-green Tyrannulet (*Phylloscartes virescens*).—Immature male (ROM 125892) 12.8 g, adult female (ROM 125891) 11 g, 28 April and 1 May 1976.

Yellow-bellied Elaenia (*Elaenia flavogaster*).—Adult female (KU 72025) 25 g, with ovary enlarged (10 × 7 mm), 16 February 1977.

Forest Elaenia (*Myiopagis gaimardii guianensis*).—Adult male (ROM 125885) 13 g, 15 May 1976; adult male (KU 71801) 12.5 g, adult female (KU 72044) 10 g, both 13 February 1977.

McConnell's Flycatcher (*Pipromorpha macconnelli*).—Two immature males (ROM 125894, ROM 126760) 2 and 12 May 1976; adult male (ROM 126505) 15 May 1976; two immature females (ROM 126584, ROM 127665) 14 and 3 May 1976, respectively; an adult male (KU 71841) 31 January 1977; two adult females (KU 71555, KU 72036) 7 and 11 February 1977. The four males' average weight was 13.1 ± 1.3 g (11–14.5 g) and the weight of the four females was 10.1 ± 2 g (8–13 g).

White-banded Swallow (*Atticora fasciata*).—Immature female (KU 71556) 10 g, 7 February 1977.

White-thighed Swallow (*Neochelidon tibialis*).—An adult female (ROM 125900) and an immature female (ROM 127659) were taken on an open slope near the Saül gas-powered generator. These two birds constitute the first records of this species in French Guiana (Dick and Barlow 1977).

Wing-banded Wren (*Microcerculus bambla*).—One unsexed adult (KU 73364) 17.5 g, 4 February 1977.

Musician Wren (*Cyphorhinus arada*).—Two adult males (ROM 125895, ROM 127660) both 22 g, 11 and 4 May 1976; adult female (KU 71527) 18 g, 5 February 1977.

Cocoa Thrush (*Turdus fumigatus*).—Adult female (KU 71830) 80 g, with ovary = 13 × 8 mm, 1 February 1977.

White-necked Thrush (*T. albicollis phaeopygus*).—Two adult males (KU 71937, KU 72022) 54 g, 44 g, both in breeding condition (testes = 13 × 8 mm, 14 × 7 mm), 31 January and 16 February 1977.

Collared Gnatwren (*Microbates collaris*).—Three adult males (ROM 125903, KU 71814, KU 71944) 11 g, 11.5 g, and 10 g, 6 May 1976, 4 and 19 February 1977, respectively.

Blue-black Grassquit (*Volatina jacarina splendens*).—Three adult males (KU 72013, KU 71955, KU 72037) 24 January, 6 and 5 February 1977; one immature male (KU 72038) 9 February 1977; adult female (KU 71818) 9 g, 25 January 1977. The four males' average weight was 9.1 ± 1 g (7.5–10 g). This species was seen in old field habitats near the airstrip and in the village. McGillivray noted that a common behavior of adult males was to jump vertically ca 35 cm off a perch while fanning the rectrices and flapping the wings several times. This behavior was repeated frequently, sometimes combined with a *zzzt* vocalization.

Chestnut-bellied Seedeater (*Sporophila castaneiventris*).—Two adult males (KU 71872, KU 72016) 6.2 g, 8.5 g, 25 January and 16 February 1977; adult female (KU 71550) 7.5 g, 5 February 1977. All three birds were in breeding condition; the males had testes measuring over 6 × 5 mm. This species was often seen in small flocks with *Volatina* in the old field habitat, especially near Saül.

Pectoral Sparrow (*Arremon taciturnus*).—Adult female (ROM 125925) 22.5 g, 14 May 1976; three adult males (KU 72065, KU 71892, KU 71823) 26 g, 28 g, and 25 g, testes measured from 9 × 9 to 11 × 6 mm, 27, 29 January and 5 February 1977, respectively; adult female (KU 71935) 31 g, 26 January 1977. This species frequented old field habitat near the airstrip.

Buff-throated Saltator (*Saltator maximus*).—Adult female (KU 71948) 46 g, largest ovum = 2 × 2 mm, 20 February 1977.

Blue-back Grosbeak (*Passerina cyanoides rothschildii*).—Two adult males (ROM 125926, ROM 125927) 6 and 4 May 1976; two adult females (ROM 127652, ROM 125928) 25 g, 28 g, 12 and 4 May 1976. All four birds were in breeding condition. Three adult males (KU 71528, KU 71950, KU 72046) 4, 9, and 13 February 1977. The testes of these birds were somewhat enlarged. The average weight of the five adult males was 27.5 ± 1 g (26–29 g).

Guira Tanager (*Hemithraupis guira nigrigula*).—Adult female (KU 71525) 9.5 g, 20 February 1977.

Yellow-backed Tanager (*H. flavicollis*).—This species was seen by McGillivray on 1 May 1976 in a mixed flock that was foraging in a breadfruit tree.

Fulvous Shrike-Tanager (*Lanio fulvus*).—Adult female (ROM 125902) 25 g, 4 May 1976. This bird was in a mixed flock foraging within 6 m of the forest floor.

Flame-crested Tanager (*Tachyphonus cristatus*).—Adult female (KU 71532) 17.5 g, 16 February 1977.

Silver-beaked Tanager (*Ramphocelus carbo*).—Three adult males (KU 71847, KU 71836, KU 72035) 20 g, 27 g, and 28 g, 29 January, 2 and 13 February 1977; two adult females (KU 71932, KU 71908) 24 g, 25 g, 30 January and 12 February 1977. The second male, with testes = 12 × 8 mm, and the latter females, with largest ovum = 3 × 2 mm, were in breeding condition.

Blue-gray Tanager (*Thraupis episcopus*).—Adult male (ROM 125901) 37 g, 10 May 1976; adult male (KU 72086) 36 g, adult female (KU 72045) 30 g, 21 and 13 February 1977. Courtship behavior by this species was observed on 27 April 1976.

Golden-bellied Euphonia (*Euphonia chrysopasta nitida*).—Adult (KU 73312) 13 g, 9 February 1977.

Turquoise Tanager (*Tangara mexicana*).—Adult male (ROM 127647) 22 g, 12 May 1976; two adult males (KU 71864, KU 71863) 19 g, 17 g, 25 January 1977; two adult females (KU 71865, KU 81821) 18.5 g, 20.5 g, 25 January and 8 February 1977.

Paradise Tanager (*T. chilensis paradisea*).—Three adult males (KU 71803, no number, KU 72023) 16 g, 17 g, and 16.5 g, 24 January, 8 and 16 February; adult female (KU 72027) 16.5 g, 16 February 1977. The male and female acquired on 16 February were in breeding condition. The male had testes measuring 12 × 12 mm and the largest ovum of the female measured 5 × 5 mm.

Spotted Tanager (*T. punctata*).—Immature male (KU 73365) 14.5 g, adult male (KU 72041) 14 g, 17 and 11 February 1977, respectively.

Bay-headed Tanager (*T. gyrola*).—Adult male (ROM 125899) 11 g, 3 May 1976.

Black-faced Dacnis (*Dacnis lineata*).—Adult male (ROM 125899) 11 g, 3 May 1976.

Blue Dacnis (*D. cayana*).—Immature male (ROM 127641) 11 g, 3 May 1976; adult male (KU 72030) 11 g, 17 February 1977; juvenile male (KU 71894) 12 g, 12 February 1977; adult female (KU 72032) 11.5 g, 16 February 1977; juvenile female (KU 72031) 12 g, 17 February 1977.

Green Honeycreeper (*Chlorophanes spiza*).—Adult female (KU 71802) 17 g, 13 February 1977.

Red-legged Honeycreeper (*Cyanerpes cyaneus*).—Adult female (ROM 125897) 13 g, immature female (ROM 125898) 13 g, both 3 May 1976; adult female (KU 72057) 15 g, adult male (KU 71947) 14 g, 9 and 18 February 1977, respectively. Both birds were in breeding condition, the male with testes = 7 × 5 mm and the female with the largest ovum = 6 × 5 mm.

River Warbler (*Phaeothlypis rivularis mesoleuca*).—Adult male (ROM 127635) 12 g, 13 May 1976.

Bicolored Conebill (*Conirostrum bicolor*).—Bird in juvenal plumage (no number) 12 g, 17 February 1977.

Bananaquit (*Coereba flaveola minima*).—Adult male (ROM 125896) 10 g, 1 May 1976; adult male (KU 72070) 7.5 g, 25 January 1977. This species was most often seen in secondary growth and the parkland habitat of Saül village.

Rufous-browed Peppershrike (*Cyclarhis gujanensis*).—Thirteen adult males (ROM 125905–ROM 125916, ROM 127650) mean weight = 26.6 ± 1.9 g (24–30 g), 1–14 May 1976; two adult females (ROM 125904, ROM 125917) 26.5 g, 25.5 g, 11 and 14 May 1976; immature

male (KU 71798) 27 g, adult female (KU 71799) 30 g, both 13 February 1977. The May birds were behaving territorially, but had not yet started to breed.

Slaty-capped Shrike-Vireo (*Vireolanius leucotis*).—Adult male (ROM 127334) 21.5 g, 10 February 1977.

Black-whiskered Vireo (*Vireo a. altiloquus*).—Immature male (ROM 127335) 23.5 g, 12 February 1977. This species has not previously been reported for French Guiana.

Red-eyed Vireo (*V. olivaceus vividior*).—Immature female (ROM 125918) 13.5 g, 12 May 1976; unsexed adult (ROM 127645) 12.8 g, 15 May 1976. Six adult males (KU 71909, KU 71910, KU 72060, KU 72061, KU 71896, KU 71800) with an average weight of 15.2 ± 0.7 g (14–16 g) were acquired from 9–13 February 1977.

Tawny-crowned Greenlet (*Hylophilus ochraceiceps luteifrons*).—Two adult males (ROM 125920, ROM 125921) 10.2 g, 10.8 g, 26 April and 11 May 1976; immature female (ROM 125919) 10 g, 26 April 1976; adult male (KU 71953) 11 g, 5 February 1977.

Green Oropendola (*Psarocolius viridis*).—Adult male (ROM 125923) 360 g, adult female (ROM 125924) 215 g, both 14 May 1976; adult male (KU 71887) 460 g, with testes = 20 × 10 mm, 22 January 1977. McGillivray recorded the call as a very melodius liquid *toodle-oodle-oo.*

Yellow-rumped Cacique (*Cacicus cela*).—Adult male (ROM 125922) 118 g, 16 May 1976; adult male (KU 71868) 102 g, adult female (KU 71921) both in breeding condition with testes = 15 × 5 mm and largest ovum = 2 × 2 mm, respectively, both 22 January 1977; five additional adult females (KU 71873, KU 71817, KU 71875, KU 71881, KU 71882) 21 January–15 February 1977. The six females' average weight was 87.8 ± 18.4 g (67–110 g). In January and February, individuals of this species were observed high in the canopy aggressively chasing each other. A tree in the open grassland outside of Saül contained about 100 pendant nests. Birds were observed copulating in this tree on 25 January. There, displaying by as many as eight individuals at once was seen.

Red-rumped Cacique (*C. haemorrhous*).—Adult male (KU 71956) 108 g, 6 February 1977. This species used the same tree as a nest-site as *C. cela,* but it was less numerous.

Yellow Oriole (*Icterus nigrogularis*).—This species was seen on 2 May 1976 near Saül by McGillivray.

Giant Cowbird (*Scaphidura oryzivora*).—Adult male (KU 71933) 174 g, with testes measuring 12 × 10 mm, 1 February 1977. Cowbirds were seen inspecting active nests of *Cacicus cela* in early February in the communal nesting tree mentioned above. Cowbirds frequented wet grassland, foraging there in large flocks with *Crotophaga ani* and both species of *Cacicus.*

CONCLUSIONS AND SUMMARY

A total of 172 species, 56 nonpasserines and 116 passerines, were taken or positively identified in the vicinity of Saül. Seventy-eight species were common to both trips; 43 were unique to the first and 49 unique to the second. Three species were reported in French Guiana for the first time. They were: *Tyrannuetes virescens, Neochelidon tibialis* and *Vireo altiloquus.*

Over 70% of the species of birds encountered at Saül preferred strata in mature forest or adjacent edge situations (Appendix).

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Appendix

Gross Habitat Preferences of Birds at Saül

Species[a]	Habitat preference										
	FC[b]	FU	FF	R	O	SG	OCF	P	G	E	OA
Tinamus major	–	–	X	–	–	–	–	–	–	–	–
Crypturellus variegatus	–	–	X	–	–	–	–	–	–	–	–
Tigrisoma lineatum	–	–	–	X	–	–	–	–	–	–	–
Elanoides forficatus	X	–	–	–	–	–	–	–	–	X	–
Harpagus bidentatus	X	–	–	–	–	–	–	–	–	X	–
Ictinia plumbea	X	–	–	–	–	–	–	–	–	X	–
Leucopternis albicollis	X	–	–	–	–	–	–	–	–	X	–
Harpia harpyja	X	–	–	–	–	–	–	–	–	–	–
Daptrius americanus	X	–	–	–	–	–	–	–	–	–	–
Ortalis motmot	–	–	–	–	–	X	–	–	–	X	–
Penelope marail	X	–	X	–	–	–	–	–	–	–	–
Psophia crepitans	–	–	X	–	–	–	–	–	–	–	–
Tringa solitaria	–	–	–	–	–	–	X	–	–	–	–
Columbina talpacoti	–	–	–	–	–	–	X	X	X	–	–
Leptotila rufaxilla	–	–	–	–	–	X	–	–	–	–	–
Ara chloroptera	X	–	–	–	–	–	–	–	–	–	–
Aratinga leucophthalmus	–	–	–	–	–	–	–	X	X	–	–
Pyrrhura picta	X	–	–	–	–	–	–	–	–	–	–
Pionus mentruus	X	–	–	–	–	–	–	–	–	–	–
P. fuscus	X	–	–	–	–	–	–	–	–	–	–
Deroptyus accipitrinus	X	–	–	–	–	–	–	–	–	–	–
Piaya cayana	X	–	–	–	–	X	–	–	–	–	–
Crotophaga ani	–	–	–	–	–	–	–	–	X	X	–
Pulsatrix perspicillata	X	–	–	–	–	–	–	–	–	X	–
Chordeiles acutipennis	–	–	–	–	X	–	–	–	–	–	–
Caprimulgus nigrescens	–	–	–	–	X	–	–	–	–	–	–
Chaetura spinicauda	–	–	–	–	–	–	–	–	–	–	X
Glaucis hirsuta	–	X	–	–	–	X	–	–	–	–	–
Phaethornis superciliosus	–	X	–	–	–	–	–	–	–	X	–
P. malaris	–	X	–	–	–	–	–	–	–	–	–
Campylopterus largipennis	–	X	–	–	X	–	–	–	–	–	–
Chlorestes notatus	–	X	–	–	–	–	–	–	–	–	–
Thalurania furcata	–	X	–	–	–	–	–	–	–	–	–
Heliothrix aurita	X	–	–	–	–	–	–	–	–	–	–
Trogon melanurus	X	–	–	–	–	–	–	–	–	–	–
T. viridis	X	X	–	–	–	–	–	–	–	–	–
T. rufus	–	X	–	–	–	–	–	–	–	–	–
T. violaceus	X	X	–	–	–	–	–	–	–	–	–
Momotus momota	X	X	–	–	–	–	–	–	–	–	–
Galbula albirostris	–	X	–	–	–	–	–	–	–	–	–
G. dea	–	X	–	–	–	–	–	–	–	X	–
Jacamerops aurea	–	–	–	X	–	–	–	–	–	–	–

Appendix
Continued

Species[a]	Habitat preference										
	FC[b]	FU	FF	R	O	SG	OCF	P	G	E	OA
Notharchus macrocrhynchus	X	–	–	–	–	–	–	–	–	–	–
Bucco tamatia	–	–	–	–	–	–	–	–	–	X	–
Malacoptila fusca	–	X	–	–	–	–	–	–	–	–	–
Monasa atra	X	–	–	–	–	–	–	–	–	–	–
Capito niger	X	–	–	–	–	–	–	–	–	–	–
Pteroglossus viridis	X	–	–	–	–	–	–	–	–	–	–
P. aracari	X	–	–	–	–	–	–	–	–	–	–
Selenidera culik	X	–	–	–	–	–	–	–	–	–	–
Ramphastos tucanus	X	–	–	–	–	–	–	–	–	–	–
Melanerpes cruentatus	X	–	–	–	–	–	–	–	–	X	–
Piculus flavigula	X	–	–	–	–	–	–	–	–	–	–
Celeus elegans	X	X	–	–	–	–	–	–	–	–	–
Dryocopus lineatus	X	–	–	–	–	–	–	–	–	–	–
Phloeoceastes rubicollis	X	–	–	–	–	–	–	–	–	–	–
Dendrocincla fuliginosa	–	X	–	–	–	–	–	–	–	–	–
D. merula	–	X	–	–	–	–	–	–	–	–	–
Glyphorhynchus spirurus	–	X	–	–	–	–	–	–	–	–	–
Dendrocolaptes certhia	–	X	–	–	–	–	–	–	–	–	–
Xiphorhynchus pardalotus	–	X	–	–	–	–	–	–	–	–	–
X. guttatus	–	X	–	–	–	–	–	–	–	–	–
Campylorhamphus procurvoides	–	X	–	–	–	–	–	–	–	–	–
Synallaxis gujanensis	–	X	–	–	–	X	–	–	–	–	–
S. cabanisi	–	X	–	–	–	–	–	–	–	–	–
Philydor ruficaudatus	–	X	–	–	–	–	–	–	–	–	–
P. erythrocercus	–	X	–	–	–	–	–	–	–	–	–
Automolus infuscatus	–	X	–	–	–	–	–	–	–	–	–
A. rubiginosus	–	X	–	–	–	–	–	–	–	–	–
A. rufipileatus	–	X	–	–	–	–	–	–	–	–	–
Sclerurus rufigularis	–	X	–	–	–	–	–	–	–	–	–
Xenops minutus	X	–	–	–	–	–	–	–	–	–	–
Cymbilaimus lineatus	–	X	–	–	–	–	–	–	–	–	–
Thamnophilus murinus	–	X	–	–	–	–	–	–	–	–	–
Thamnomanes ardesiacus	–	X	–	–	–	–	–	–	–	–	–
T. caesius	–	X	–	–	–	–	–	–	–	–	–
Myrmotherula gutturalis	–	X	–	–	–	–	–	–	–	–	–
M. axillaris	–	X	–	–	–	–	–	–	–	–	–
M. longipennis	X	–	–	–	–	–	–	–	–	–	–
M. menetriesii	X	–	–	–	–	–	–	–	–	–	–
Microrhopias quixensis	–	X	–	–	–	–	–	–	–	–	–
Cercomacra tyrannina	–	X	–	–	–	–	–	–	–	–	–
Myrmoborus leucophrys	–	X	–	X	–	–	–	–	–	–	–
Hypocnemis cantator	–	X	X	–	–	–	–	–	–	–	–

Appendix
Continued

Species[a]	Habitat preference										
	FC[b]	FU	FF	R	O	SG	OCF	P	G	E	OA
Percnostola rufifrons	–	X	X	–	–	–	–	–	–	–	–
Myrmeciza ferruginea	–	–	X	–	–	–	–	–	–	–	–
M. atrothorax	–	X	X	–	–	–	–	–	–	X	–
Pithys albifrons	–	X	X	–	–	–	–	–	–	–	–
Gymnopithys rufigula	–	X	X	–	–	–	–	–	–	–	–
Hylophylax poecilonota	–	X	–	–	–	–	–	–	–	–	–
Formicarius colma	–	–	X	–	–	–	–	–	–	–	–
F. analis	–	–	X	–	–	–	–	–	–	–	–
Hylopezus macularius	–	–	X	–	–	–	–	–	–	–	–
Conopophaga aurita	–	–	X	–	–	–	–	–	–	–	–
Corythopis torquata	–	–	X	X	–	–	–	–	–	–	–
Lipaugus vociferans	X	X	–	–	–	–	–	–	–	–	–
Tityra cayana	X	–	–	–	–	–	–	–	–	–	–
Cotinga cayana	X	–	–	–	–	–	–	–	–	–	–
Querula purpurata	X	–	–	–	–	–	–	–	–	–	–
Perissocephalus tricolor	X	–	–	–	–	–	–	–	–	–	–
Pipra erythrocephala	–	X	–	–	–	–	–	–	–	–	–
P. pipra	–	X	–	–	–	–	–	–	–	–	–
P. serena	–	X	–	–	–	–	–	–	–	–	–
Manacus manacus	–	X	–	–	–	–	–	–	–	–	–
Tyranneutes virescens	–	X	–	–	–	–	–	–	–	–	–
Piprites chloris	X	–	–	–	–	–	–	–	–	–	–
Schiffornis turdinus	–	X	–	–	–	–	–	–	–	–	–
Colonia colonus	X	–	–	–	–	–	–	–	–	–	–
Muscivora tyrannus	–	–	–	–	X	–	–	X	–	–	–
Tyrannus melancholicus	–	–	–	–	X	–	–	X	–	X	–
Empidonomus varius	–	–	–	–	X	–	–	X	–	X	–
Legatus leucophaius	–	–	–	–	X	–	–	X	–	X	–
Conopias parva	–	–	–	–	–	X	–	–	–	X	–
Megarhynchus pitangua	X	–	–	–	–	–	–	–	–	X	–
Platyrinchus platyrhynchos	–	X	–	–	–	–	–	–	–	–	–
Tolmomyias assimilis	–	X	–	–	–	–	–	–	–	–	–
T. poliocephalus	X	X	–	–	–	–	–	–	–	–	–
Myiozetes cayanensis	–	–	–	–	X	–	–	X	–	X	–
Pitangus sulphuratus	–	–	–	–	X	–	–	X	–	X	–
Attila spadiceus	–	X	–	–	–	–	–	–	–	–	–
Rhytipterna simplex	X	–	–	–	–	–	–	–	–	–	–
Laniocera hypopyrrha	–	X	–	–	–	–	–	–	–	–	–
Terenotriccus erythrurus	–	X	–	–	–	–	–	–	–	–	–
Myiobius barbatus	X	X	–	–	–	–	–	–	–	–	–
Onychorhynchus coronatus	–	X	–	X	–	–	–	–	–	–	–
Ramphotrigon ruficauda	–	X	–	–	–	–	–	–	–	–	–

APPENDIX
CONTINUED

Species[a]	Habitat preference										
	FC[b]	FU	FF	R	O	SG	OCF	P	G	E	OA
Todirostrum cinereum	–	–	–	–	–	X	–	–	–	X	–
Idioptilon zosterops	X	X	–	–	–	–	–	–	–	–	–
Phylloscartes virescens	X	–	–	–	–	–	–	–	–	–	–
Elaenia flavogaster	–	–	–	–	X	–	–	X	–	X	–
Myiopagis gaimardii	X	X	–	–	–	–	–	–	–	–	–
Pipromorpha macconnelli	–	X	–	–	–	–	–	–	–	–	–
Atticora fasciata	–	–	–	X	–	–	–	–	–	–	–
Neochelidon tibialis	–	–	–	–	–	–	–	–	–	–	X
Microcerculus bambla	–	X	–	–	–	–	–	–	–	–	–
Cyphorhinus arada	–	X	–	–	–	–	–	–	–	–	–
Turdus fumigatus	–	X	–	X	–	–	–	–	–	–	–
T. albicollis	–	X	X	–	–	–	–	–	–	–	–
Microbates collaris	–	X	–	–	–	X	–	–	–	–	–
Volatina jacarina	–	–	–	–	–	–	X	–	X	X	–
Sporophila castaneiventris	–	–	–	–	X	–	–	–	X	X	–
Arremon taciturnus	–	–	X	–	–	–	–	–	–	–	–
Saltator maximus	–	–	X	–	–	X	–	–	–	X	–
Passerina cyanoides	–	X	–	X	–	–	–	–	–	–	–
Hemithraupis guira	X	–	–	–	–	–	–	–	–	–	–
H. flavicollis	X	–	–	–	–	–	–	–	–	–	–
Lanio fulvus	X	–	–	–	–	–	–	–	–	–	–
Tachyphonus cristatus	X	–	–	–	–	–	–	–	–	–	–
Ramphocelus carbo	–	–	–	–	–	X	–	–	–	X	–
Thraupis episcopus	–	–	–	–	–	–	–	X	–	X	–
Euphonia chrysopasta	–	–	–	–	–	X	–	–	–	–	–
Tangara mexicana	–	–	–	–	–	–	–	X	–	–	–
T. chilensis	X	–	–	–	–	–	–	–	–	–	–
T. punctata	X	–	–	–	–	–	–	–	–	–	–
T. gyrola	X	–	–	–	–	–	–	–	–	–	–
Dacnis lineata	X	–	–	–	–	–	–	–	–	–	–
D. cayana	X	–	–	–	–	–	–	–	–	X	–
Chlorophanes spiza	X	–	–	–	–	–	–	–	–	–	–
Cyanerpes cyaneus	X	–	–	–	–	–	–	–	–	–	–
Phaeothlypis rivularis	–	–	X	X	–	–	–	–	–	–	–
Conirostrum bicolor	X	X	–	–	–	–	–	–	–	–	–
Coereba flaveola	–	–	–	–	–	–	–	X	–	X	–
Cyclarhis gujanensis	–	–	–	–	–	–	–	X	–	X	–
Vireolanius leucotis	X	–	–	–	–	–	–	–	–	–	–
Vireo altiloquus	X	–	–	–	–	–	–	–	–	–	–
V. olivaceus	X	–	–	–	–	–	–	–	–	–	–
Hylophilus ochraceiceps	–	X	–	–	–	–	–	–	–	–	–
Psarocolius viridis	X	–	–	–	–	–	–	–	–	–	–

Appendix
Continued

Species[a]	Habitat preference										
	FC[b]	FU	FF	R	O	SG	OCF	P	G	E	OA
Cacicus cela	X	–	–	–	–	–	–	–	–	X	–
C. haemorrhous	X	–	–	–	–	–	–	–	–	X	–
Icterus nigrogularis	–	–	–	X	–	X	–	–	–	–	–
Scaphidura oryzivora	X	–	–	–	–	–	–	–	–	X	–

[a] Birds near Saül showed percent habitat and niche preferences based on number of species per habitat type/172 × 100 as follows: undergrowth—26.9; canopy—23.4; mid-canopy–forest floor—7.8; canopy–edge—7.2; forest floor—5.4; open parkland–edge—4.8; undergrowth–forest floor—3.0; undergrowth–riparian—2.4; undergrowth–second—2.4; secondary–edge—2.4; grassland–edge—1.8; undergrowth–edge—1.2; riparian—1.2; open—1.2; secondary—1.2; forest floor–riparian—1.2; open aerial—1.2; open clearing forest—0.6; parkland—0.6; secondary canopy—0.6; forest floor–secondary–edge—0.6; forest floor–canopy—0.6.

[b] Acronyms for habitats are as follows: FC = forest canopy, FU = forest undergrowth, FF = forest floor, R = riparian, O = open airstrip, SG = secondary growth, OCF = open clearing in forest, P = parkland, G = grassland, E = edge, OA = (aerial) open airstrip.

COLOR PLATE

Inclusion of the colorplate frontispiece of Chestnut-bellied Gnatcatchers (*Conophaga aurita*) has been made possible through an endowment established by George Miksch Sutton (1896–1982). Painting by John P. O'Neill.

CHANGE IN EDITOR

Dr. Keith A. Bildstein will be serving as the Editor of The Wilson Bulletin beginning with Volume 97. As of 15 May 1984, all manuscripts submitted for publication in the journal should be sent to him at the **Department of Biology, Winthrop College, Rock Hill, SC 29733.** All manuscripts received prior to 15 May 1984 will continue to be processed by Dr. Jon C. Barlow.

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ECOLOGY OF THE WEST INDIAN RED-BELLIED WOODPECKER ON GRAND CAYMAN: DISTRIBUTION AND FORAGING

ALEXANDER CRUZ AND DAVID W. JOHNSTON

The West Indian Red-bellied Woodpecker (*Melanerpes superciliaris*) is widely distributed in the West Indian region, occurring on Cuba, Isle of Pines, Grand Cayman, Grand Bahama, Abaco, and San Salvador (Watling's) Island. Because of its extensive distribution in contrast to other Antillean woodpeckers (Bond 1956, Cruz 1974), *M. superciliaris* is an exceptionally good species for studies of geographic variation in foraging behavior, in differential sexual foraging related to regional variation in quality and quantity of food, and in intensity of interactions with other woodpeckers and species of similar foraging adaptations. To date, *M. superciliaris* remains little known; the primary literature, with the exception of the Grand Cayman subspecies (*M. s. caymanensis*), consists almost entirely of brief accounts (Gundlach 1893, Allen 1905, Bangs and Zappey 1905, Riley 1905, Barbour 1923, Paulson 1966, Brudenell-Bruce 1975, Garrido and Garcia Montaña 1975, Miller 1978, King 1981). Johnston (1970, 1975) and Cruz and Johnston (1979) summarized aspects of the ecology of *M. superciliaris* on Grand Cayman, and Cruz (1974) discussed the probable evolution and fossil record of *M. superciliaris*.

The present study of *M. superciliaris* was initiated on Grand Cayman in 1965 and continued intermittently until 1974, covering all seasons. A total of 800 h was spent in the field. The objectives of these investigations were to obtain data on: (1) distribution and habitat preferences, (2) food and foraging ecology, and (3) differential feeding between the sexes.

STUDY AREAS

Grand Cayman lies approximately 290 km south of Cuba, 310 km west of Jamaica, and 480 km NE of Honduras, the nearest point in Central America. Much of Grand Cayman (185 km^2) is less than 5 m above sea level. Temperatures are fairly constant (mean annual high 30°C) and annual mean precipitation is 1549 mm (Johnston 1975). A dry season extends from November to April. To obtain as complete a picture as possible of the ecology of *M. superciliaris*, we visited many distinct habitats (strand woodland or sea grape-almond woodland, mangrove woodland, open pastures, scrub woodland, limestone forest, and town and house sites). Scrub woodland consists of abandoned and other cleared areas that revert to woods consisting of species such as maiden plum (*Comocladia pinnatifolia*), red birch (*Bursera simaruba*), and logwood (*Haematoxylum campechianum*). Open and, later, dense stands of nearly pure logwood develop on drier upland sites. Older stages frequently include thatch palm (*Thrinax argentea*) and red birch (logwood-thatch palm-red birch association). The woodland averages about 6 m in height. Investigations were done in the logwood forest

and in the logwood-thatch palm-red birch association. For a more detailed description of these areas see Johnston (1975) and Cruz and Johnston (1979).

METHODS

Population density.—Traditional techniques for measuring bird populations, such as transect counts or territory mapping, proved to be impossible in the rough and uneven terrain of Grand Cayman. The absence of trails for accurately measuring distances in most of the woods made it difficult to measure population densities precisely. A semi-quantitative method was devised to provide relative indices of abundance. Ten censuses, each about 2-h long, were taken in the early morning in representatives of each of the major ecological formations during December, April, May, June, and August of all years. After all birds recorded during each census were counted, relative abundance scores were derived as follows: U (uncommon), 5–20 individuals/20 h; FC (fairly common), 20–100 individuals/20 h; C (common), 100–200 individuals/20 h.

Foraging ecology.—Habitat use, foraging, and feeding methods of the birds in the study areas were studied by adapting methods used by MacArthur (1958), Cody (1974), and Cruz (1977). We moved about the study areas on a systematic basis, observing as many different birds at various times of the day as possible. Individuals were followed as long as they remained in sight, which in some of the stands was not usually longer than 60 sec. In some cases, however, birds were observed for several minutes and a sequence of foraging maneuvers was obtained. An individual observation was terminated if the bird changed behavior. A Chi-square contingency test was used to evaluate the frequency of occurrence in each of the categories. Only differences at the $P < 0.05$ level of significance were accepted.

We calculated overlap in foraging behavior of males and females with Schoener's (1970) equation:

$$\% \text{ overlap} = 100\ [1 - 0.5\ \Sigma\ (P_{x,i} - P_{y,i})]$$

where $P_{x,i}$ and $P_{y,i}$ are the respective frequencies for males and females in each class for a given type of behavior. An overlap of 100% indicates that the sexes acted identically in regard to the type of behavior examined, whereas 0% overlap indicates completely different behavior.

Foods.—We collected 14 adults on Grand Cayman for stomach analyses. The stomach and intestinal tract were removed soon after death and preserved in 75% alcohol. Later the foods therein were separated taxonomically and analyzed by volume and by frequency of occurrence. Food volumes were ascertained with reasonable accuracy by noting the displacement of water in a graduated cylinder accurate to 0.1 ml. Whole invertebrates were identified at least to family; fragmented insects were identified to order in nearly all cases and often to family. Similar methods were used to identify fruits found in the stomach.

Body measurements.—Morphological data were obtained by standard mensural methods to see if any sexual dimorphism in body structures of possible ecological significance existed. Bill length was measured from the anterior margin of the nostril to the tip; the tarsometatarsus was measured from its posterior proximal end to the distal edge of the most distal unbroken scale crossing the bases of the two forward toes. Measurements were done to the nearest 0.1 mm with vernier calipers. We weighed all the specimens to the nearest 0.1 g with a triple beam balance.

RESULTS

Habitat, distribution and abundance.—*M. superciliaris* occurred over the island in all forests, from mangrove woodlands to dense limestone

TABLE 1

RELATIVE ABUNDANCE[a] OF *MELANERPES SUPERCILIARIS* IN VARIOUS HABITATS ON GRAND CAYMAN

Habitat	December	April–May	June	July
Strand woodland[b]	NO	NC	U	NO
Mangrove swamps	U	NC	NO	U
Logwood forests	U	NC	U	NC
Scrub forests[c]	U	FC	NC	FC
Limestone forests	C	FC	NC	FC
Town and house sites	U	U	NC	U

[a] NO = not observed, NC = not censused, U = uncommon (5–20 individuals 20 h), FC = fairly common (20–100 individuals 20 h), C = common (100–300 individuals 20 h).
[b] Also called sea grape–almond woodland.
[c] Logwood and logwood–thatch palm–red birch associations.

forest. The birds were most numerous in the limestone forests and scarcest in the mangrove and ruderal sites (Table 1). *M. superciliaris* occurred in habitats where the diversity of tree species ranged from low (one or two species), such as mangrove and logwood forests, to high (10–15 species), such as limestone forests. The birds were absent from pastures and cultivated areas, despite scattered trees.

Measurements.—Besides the sexual differences in degree of redness of the head region (crown to hindneck scarlet in male, but only nape and hindneck red in female), the mean values for weight, culmen, and tarsometatarsal length were found to be greater in males than in females (Table 2). The overall variation for bill length was slightly greater among females and for tarsometatarsal length among males (Table 2). Weights varied more in males than females. Despite the overlapping ranges found for all the parameters measured, the intersexual differences between the mean values were significant at $P < 0.001$ level for culmen length ($t = 5.66$, df = 21), weight ($t = 3.70$, df = 14), and tarsometatarsal length ($t = 2.98$, df = 19).

The degree of intersexual difference (expressed as the difference in mean values in relation to the mean values for males) in bill length and in weight was greater than that found for tarsometatarsal lengths (Table 2). The greater degree of sexual dimorphism found in bill length and in weight is emphasized by the coefficient of difference (derived from the mean difference between the sexes divided by their combined standard deviations) and the corresponding joint non-overlap values (Dunn and Everitt 1982) which indicates the proportion of the individuals of each sex which does not overlap a corresponding proportion of those of the other sex. The coefficients indicate a 91% joint non-overlap for bill length (C.D. = 1.35)

TABLE 2

MEAN WEIGHTS AND MEASUREMENTS OF *MELANERPES SUPERCILIARIS CAYMANENSIS*[a]

	Males			Females			% difference in mean measurements	Coefficient of difference	% joint nonoverlap
	N	Mean ± SE (range)	C.V.[b]	N	Mean ± SE (range)	C.V.[b]			
Bill (mm)	17	26.4 ± 0.30 (23.5–28.0)	4.87	6	23.2 ± 0.5 (21.7–24.5)	5.24	12.1	1.35	91
Tarsus (mm)	16	23.97 ± 0.28 (21.8–26.1)	4.40	5	22.4 ± 0.44 (21.0–23.1)	3.9	6.5	0.81	77
Weight (g)	11	84.2 ± 2.5 (71.3–99.3)	9.37	5	71.0 ± 1.49 (67.3–73.5)	4.2	15.7	1.21	89

[a] Data from Ridgway (1914) and this study.
[b] Coefficient of variation.

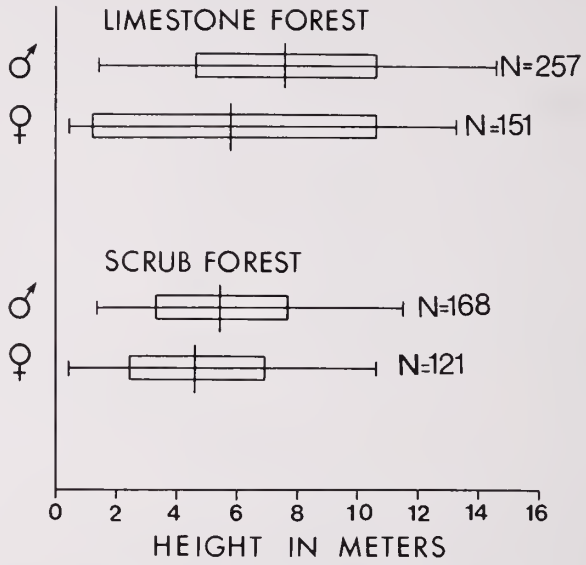

FIG. 1. Foraging heights of male and female *Melanerpes superciliaris*. Open rectangles represent 1 SD to either side of the mean; the line indicates the range.

and an 89% of joint non-overlap in weight (C.D. = 1.213) for *M. s. caymanensis* (Table 2).

Foraging heights.—Detailed foraging ecology information was obtained in two distinct habitats—scrub forest (average tree height 6 m) and dry limestone forest (average tree height 9 m). In general, males foraged significantly higher than females ($P < 0.05$). In the scrub forest the mean foraging heights for males and females were 5.39 and 4.49 m ($t = 3.3$, df = 287), respectively, and in the limestone forest the mean foraging heights for males and females were 7.69 and 5.83 ($t = 4.96$, df = 406), respectively (Fig. 1). Overlaps in use of foraging heights by the sexes were 80.4% and 90.9%, respectively, for the scrub and limestone forests. Both sexes used similar foraging heights, but at different frequencies.

Foraging zones.—Table 3 summarizes the pooled results for the scrub and limestone forests of the total number of times *M. superciliaris* was noted in the different foraging zones—trunk, inner, and outer portions of the crown. *M. superciliaris* used different zones preferentially, but with the exception of the lower trunk, no statistically significant intersexual differences in the use of these zones (Chi-square contingency tests) were noted (Table 3). The inner branches were most commonly used as a foraging zone with the trunks being used the least. Although both sexes

TABLE 3

FORAGING ZONES OF *MELANERPES SUPERCILIARIS* ON GRAND CAYMAN

Habitat	Tree zone	Percent use		Percent difference
		Male	Female	
Pooled data		421[a]	272	
from scrub	Trunk			
and limestone	lower	8.2	13.4	5.2[b]
forests	upper	6.8	7.3	0.5
	Branches			
	inner	47.05	42.2	4.9
	outer	38.00	37.3	0.7

[a] Number of observations.

[b] Chi-square values: lower trunk ($\chi^2 = 4.32$, df = 1, $P < 0.05$), upper trunk ($\chi^2 = 0.16$, df = 1, NS), inner branches ($\chi^2 = 1.37$, df = 1, NS), outer branches ($\chi^2 = 0.01$, df = 1, NS).

used the lower trunk, females tended to use this zone significantly more, 13.4% vs 8.2%, respectively (Table 3). Overlaps in the use of zones by the sexes was 94.5%.

Foraging behavior.—The pooled results for both sexes from both study areas indicate that the predominant foraging methods are fruit-eating (37.7%), arboreal gleaning (23.9%), probing (20.6%), and pecking (13.4%). Probing into epiphytes accounted for the rest of the foraging methods (Table 4). Males pecked more frequently than females, and females gleaned more frequently. These differences were statistically significant (Chi-square contingency tests). Overlap in use of methods by the sexes was 84.6%, however, differences in frequencies of use of probing, fruit-eating, and epiphytic probing were not statistically significant (Table 4).

In probing, both the bill and the tongue were used to explore natural cavities and accumulations of plant materials. Cavities in which the woodpeckers probed included fissures and cracks in the bark, knot holes, weathered holes previously excavated by woodpeckers, holes in ends of rotten or dying branches, and stumps. Accumulation of plant material included debris between trunks and lateral trunks. Pecking for food was confined mainly to dead or dying portions of the tree, ranging from large trunks to the outer branches. In pecking, *M. superciliaris* assumes the woodpecker stance described by Spring (1965) for some North American woodpeckers. The whole body is held away from the tree trunk and the blow delivery momentum appears to come from regions posterior to the neck, although it appears that the neck also plays a role. Gleaning consisted in search along the limb and trunk surfaces for invertebrates and use of the tongue to capture prey.

TABLE 4

FORAGING BEHAVIOR OF *MELANERPES SUPERCILIARIS* ON GRAND CAYMAN

Habitat	Method	Percent use		Percent difference
		Male 421[a]	Female 272	
Pooled data	Pecking	19.4	7.3	12.1[b]
from scrub	Probing	20.9	20.3	0.6
and limestone	Gleaning	17.4	30.5	13.1
forests	Fruits	39.1	36.3	2.8
	Epiphytes	3.3	5.7	2.4

[a] Number of observations.

[b] Chi-square values: pecking ($\chi^2 = 14.2$, df = 1, $P < 0.001$), probing ($\chi^2 = 0.008$, df = 1, NS), gleaning ($\chi^2 = 15.5$, df = 1, $P < 0.001$), fruits ($\chi^2 = 0.42$, df = 1, NS), epiphytes ($\chi^2 = 1.5$, df = 1, NS).

Although *M. superciliaris* is structurally specialized to obtain food by pecking, fruit-eating constitutes a greater proportion of the pooled foraging behavior than pecking, the former accounting for 37.7% and the latter for 13.4%. In addition, the results of the stomach analyses indicate an even greater use of fruits (Table 5) than shown by the foraging behavior. *M. superciliaris* showed considerable agility in moving over the outer branches of trees where most of the fruits grew. Birds often balanced between two limbs, with legs spread apart, holding one branch with each foot, and reaching out for the fruits. Sometimes individuals flew to a clump, clung to the fruits, and plucked them. Small fruits (<30 mm) were plucked and swallowed, and if the fruits were small (10 mm) it was not uncommon to see woodpeckers with more than one fruit in the bill at a time. If the fruit was large (>30 mm) (e.g., papaya), the bird first pecked a hole in it and then used the bill and tongue to probe and feed on the fleshy pulp. We recorded 11 different species of fruits eaten by *M. superciliaris*. Fruits from trees of the families Caricaceae, Moraceae, and Burseraceae figured prominantly.

Stomach analyses.—The stomach content overlap indices (93%), calculated on frequency of families in the diet, suggest that males and females took similar food items. Therefore, the diets of males and females were combined in the analysis of diet (Table 5). Evidence of differential food-size selection was not found. In *M. superciliaris* diets, both animal and vegetable matter are well represented, comprising 56.0% and 44.0%, respectively, of the total volume, and 64.3% and 78.6%, respectively, of the percent occurrence (Table 5). A striking general result of the present study is the demonstration of the major role played by vegetable material

TABLE 5

FOOD ITEMS FOUND IN THE STOMACHS OF *MELANERPES SUPERCILIARIS*

	Percent (14)[a]			Percent (14)[a]	
	Occurrence	Volume		Occurrence	Volume
Mollusca	7.1	1.8	Plantae		
Gastropoda	7.1	1.8	Moraceae	21.4	7.2
Pulmonata	7.1	1.8	*Ficus*	21.4	7.2
Arthropoda	64.3	46.7	Myrtaceae	7.1	1.3
Arachnida	14.3	2.2	*Eugenia*	7.1	1.3
Araneidae	14.3	2.2	Caricaceae	57.1	29.3
Insecta	64.3	44.5	*Carica*	57.1	29.3
Orthoptera	35.7	31.5	*Burseraceae*	14.3	4.1
Gryliidae	28.6	21.0	*Bursera*	14.3	4.1
Acrididae	21.4	10.5	Passifloraceae	2.1	2.1
Coleoptera	21.4	5.8	*Passiflora*	2.1	2.1
Curculionidae	7.1	2.2			
Tenebrionidae	7.1	3.6			
Hymenoptera	14.3	4.2			
Formicidae	7.1	3.1			
Vespidae	7.1	1.1			
Vertebrata	14.3	7.5			
Amphibia	7.1	3.3			
Hylidae	7.1	3.3			
Reptilia	14.3	4.2			
Gekkonidae	7.1	4.2			
Total	64.3	56.0		78.6	44.0

[a] Sample size of stomachs.

(fruits) in the diet of a member of a family considered to be primarily insectivorous.

The animal food embraced 5 classes, 7 orders, and 10 families. Insects were most important in the woodpecker diet, comprising 44.5% by total volume. The most important insect taxa were orthoptera, accounting for 31.5% of the total volume. The proportion of prey found in the stomachs (56.0%) is in close agreement with observations of foraging methods, where gleaning, probing, and pecking for prey accounted for 57.6% of the total pooled foraging. Plant materials consisted of fruits and seeds representing four identified families and four genera. The family Caricaceae was the most important in the diet, their pulp and seeds accounting for 29.3% of the total volume. Other plants important in the diet (in percent

of total volume) were fruits and seeds of the families Moraceae (7.2%) and Burseraceae (4.1%).

DISCUSSION AND CONCLUSIONS

Among woodpeckers, in general, females tend to be smaller than males in several mensural characteristics (Selander and Giller 1963, Selander 1966). Selander and Giller (1963) found that the degree of sexual dimorphism in culmen length of some *Melanerpes* woodpeckers is greater than any other morphological characteristic compared—this was especially true in some West Indian forms, e.g., Hispaniolan Woodpecker (*M. striatus*) of Hispaniola, Guadeloupe Woodpecker (*M. herminieri*) of Guadeloupe, and the Puerto Rican Woodpecker (*M. portoricensis*) of Puerto Rico. The proposal of Selander and Giller (1963), that this disproportionate degree of sexual dimorphism in culmen length is adaptive and serves to alleviate intersexual competition for food, was later confirmed by Selander (1966) for *M. striatus* and by Wallace (1974) for *M. striatus* and *M. portoricensis.* Subsequently, various investigators have quantified foraging differences between the sexes in woodpeckers (Kilham 1965, 1970; Ligon 1968a, b; Jackson 1970; Koch et al. 1970; Short 1970a, b; Willson 1971; Kisiel 1972; Austin 1976; Hogstad 1976, 1978; Jenkins 1979; Winkler 1979; Ramey 1980; Williams 1980; Hooper and Lennartz 1981). The sexes may forage in different strata, use different foraging techniques, or take food items of different sizes.

When the differences found in those morphological characters that are important for feeding (e.g., bill size) in *M. superciliaris* are compared with the intersexual differences in foraging behavior, a relationship between dimorphism and feeding niches seems evident. Compared with the female, the male was often seen pecking, a not unexpected finding considering the greater bill length in the male. The larger-billed males are probably better adapted for pecking and feeding at the deeper levels of the bark and cambial layer. Compared to males, the female does less pecking and more gleaning. Presumably, the female with the smaller bill is less specialized for pecking.

Selander (1966) and Koplin (1967) found that the smaller sex in *Melanerpes* species and *Picoides tridactylus* foraged upon smaller substrates. We expected to find the smaller sex (female) of *M. superciliaris* foraging upon smaller substrates also (i.e., outer branches and higher up in the trees). The size difference between the sexes of *M. superciliaris* is statistically significant, and, therefore, should be great enough to have an effect on substrate selection. With the exception of the lower trunk, there were no statistically significant differences in the use of the zones, although females used the upper trunk and inner branches more than the males.

Differences in the foraging heights were statistically significant, with the males foraging higher than the females. These differences were more apparent when the sexes were feeding together in the same tree. Males of *M. superciliaris* are larger and presumably dominant to the females. Accordingly, the male should use this presumed advantage (dominance) when feeding together to forage in the more productive portions of the tree with the females giving way and feeding in the less desirable areas. On Grand Cayman, the more productive sites were the inner and outer branches where fruits, bromeliads, and many dead branches were located. The trunk (lower portions) was suboptimal in this respect.

The most frequently cited presumed advantages for intersexual foraging differences in woodpeckers are a reduction in intraspecific competition for food and a concomitant reduction in intersexual aggression (Selander 1966, Ligon 1968a, Wallace 1974, Hogstad 1976, Jackson 1979, Hooper and Lennartz 1981). These adaptive advantages may also be of major significance to *M. superciliaris* in their daily activities; pairs were often seen in close proximity maintaining contact vocally, and in some instances were observed feeding in the same tree. As suggested by Wallace (1974) and Hooper and Lennartz (1981) for other species, sexual partitioning of the foraging resource is a possible mechanism for facilitating social organization of *M. superciliaris* by reducing intersexual aggression and competition. It is interesting to note that Wallace (1974) found a positive correlation between foraging proximity and sexual dimorphism in bill length in several melanerpine woodpeckers. The strong correlation, also observed in this study for *M. superciliaris,* may be associated with foraging association of the sexes by permitting a finer division of the feeding niche.

The observations presented here suggest that male and female *M. superciliaris* on Grand Cayman Island differ in some types of feeding behaviors and may in this manner make more effective use of their environment. As pointed out by Kilham (1965), Selander (1966), Ligon (1968a), and Koch et al. (1970), however, regional differences in intraspecific foraging ecology may be expected among species with wide geographic ranges (e.g., Hairy Woodpecker [*Picoides villosus*], Red-cockaded Woodpecker [*P. borealis*], and White-headed Woodpecker [*P. albolarvatus*]). This is also probably the case for *M. superciliaris,* which occurs in different islands with a diversity of habitats present. In the Bahamas, for example, *M. superciliaris* also occurs in pine habitats, areas not present in Grand Cayman. Such regional differences in intraspecific foraging behavior may also be due to other factors including the quantity and quality of food available, sets of avian and other competitors, climatic factors, etc. Additionally, such studies as noted by Kilham (1965), Wallace (1974), Conner (1979), and Winkler (1979) must allow for effects of seasonal changes in popu-

lations of both predator and prey species as well as in those of competitors. In Hispaniola, Wallace (1974) found greater sexual differences in foraging in the dry winter months, considered to be a time of low food abundance. Less sexual difference in foraging mode was found in this species in ecologically more complex areas.

The large and diverse numbers of animal and plant species eaten strongly suggest that *M. superciliaris* is exceedingly diverse and opportunistic in its feeding habits, taking nearly all the animal and fruit material (within a certain size range) that it encounters while foraging. Fruit size is probably not of great importance, as the woodpecker uses its tongue and bill to feed on the fleshy pulp of large fruits. The generalist food habits of *M. superciliaris* are not surprising when one considers the following. Three broad ecological types may be recognized among North American woodpeckers (Bock 1970), each centering on a type of food niche. The first group, the "ground type," is represented by the flickers. Second is a group of "classical" woodpeckers (*Dendrocopos, Picoides, Dryocopus,* and *Campephilus*), consisting of species that obtain their food largely by pecking and scaling living or dead wood to extract insect prey. Finally, relatively omnivorous species (in *Melanerpes*) are opportunistic in their feeding habits and obtain a majority of their food by non-pecking means. The opportunistic feeding habits of this species, the sexual difference, and the partial intersexual differences in the feeding niche found in *M. superciliaris* may perhaps be considered as being one of several adaptations in this Caribbean species which enables it to occupy a diverse number of habitats.

SUMMARY

The West Indian Red-bellied Woodpecker (*Melanerpes superciliaris*) is resident throughout Grand Cayman in suitable habitats from mangrove to dense limestone forests. Despite the overlapping ranges found for weight, culmen, and tarsometatarsal length, mean values were significantly higher in males than in females. When the differences found in those characters that are important for feeding (e.g., bill size) in *M. superciliaris* are compared with the intersexual differences in foraging behavior, a relationship between dimorphism and feeding niches seems evident. The predominant foraging methods are fruit-eating (37.7%), gleaning (23.9%), probing (20.6%), and pecking (13.4%). Compared with the female, the male was often seen pecking. The larger-billed males are probably better adapted for pecking and feeding in the deeper levels of the bark and cambial layer. The intersexual differences in gleaning were statistically significant, the females gleaning more frequently. We expected to find the smaller female foraging upon smaller substrata (i.e., outer branches and higher up in trees). With the exception of the lower trunk, there were no statistical differences in the use of zones, although the females also tended to use the upper trunk and inner branches with a greater frequency than the males. There were significant differences in the foraging heights, with the males foraging higher. In their daily activities, pairs of *M. superciliaris* were often seen in close proximity, maintaining contact vocally. Sexual partitioning of the

foraging resources is a possible mechanism of facilitating social organization in *M. superciliaris* by reducing intersexual aggression and competition.

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INTERFERENCE AND EXPLOITATION IN BIRD COMMUNITIES

Brian A. Maurer

The past two decades of research on the population ecology of birds have produced a great deal of activity and controversy in relation to the role of competition in determining which species can live together in the same habitat (Wiens 1977, Diamond 1978, Schoener 1982). It has long been realized that there are at least two ways in which competition between species can occur (Miller 1967, Morse 1980a). The first is commonly called exploitative competition and involves the removal of resources by one species, leaving less for competing species. The second type of competition, termed interference, includes processes by which the activities of one species prevent the use of resources by other species. Authors of nearly every study of competition in bird communities have either assumed that all types of competition lead to the same ecological and evolutionary consequences or that competition involves only exploitation.

Recent published research on competition has been based almost exclusively on the Lotka-Volterra paradigm of population growth (MacArthur 1972). MacArthur (1958), following the early insights of Lack (see Lack 1971), was one of the first researchers to bring a body of earlier mathematical arguments (e.g., Lotka 1925, Gause 1934) to bear on the problem of species coexistence in relatively uniform habitats. MacArthur's (1958) point was that each of the birds in the community he studied had features related to their foraging activities which prevented them from using exactly the same resources, and hence they could live in the same community. A number of subsequent studies (e.g., Cody 1974, Schoener 1974) attempted to extend and verify MacArthur's (1972) ideas, summarized in his book.

This attention to competition as a mechanism of "structuring" bird communities, and communities in general, led to a growing consensus regarding the mechanisms that regulated the distribution and abundance of organisms (Cody and Diamond 1975). However, Wiens (1976, 1977) posed important questions regarding the developing theory of community structure. He suggested that the environments in which bird communities existed varied much more than was commonly recognized by community theory. Though Fretwell (1972) had made attempts to incorporate environmental variability due to seasonality into the theory, Wiens (1977) implied that the problem was too serious to be incorporated into the existing theory. Responses to Wiens' criticisms by influential ecologists

(Diamond 1978, Cody 1981, Schoener 1982), though appealing, have not been convincing. Currently, many authors studying a variety of bird communities are equally divided in the interpretation of their results (e.g., Cody 1978; Wiens and Rotenberry 1979, 1980, 1981a, b; Rotenberry and Wiens 1980a, b; Noon 1981; Rusterholz 1981; Collins et al. 1982; Nudds 1982; Rosenberg et al. 1982; Toft et al. 1982).

In the following paragraphs, I suggest that a great deal of the present confusion has been derived from a mistaken impression, due to use of the Lotka-Volterra competition model, that the ecological and evolutionary results of exploitative competition and interference competition are the same. While conceptualizing and rigorously defining the ecological consequences of these differing competitive processes may not provide a unifying basis for explaining why bird species occur in the combinations they do in the natural world, I believe it is important that ideas be as clearly defined as possible in order to facilitate the formation of adequate hypotheses. The formulation and testing of rigorous hypotheses for local species assemblages promises to be more fruitful for the progress of avian ecology than a new generation of complex, abstract mathematical models (Pielou 1981, Simberloff 1982).

THE CONVENTIONAL PARADIGM

Both the proponents and antagonists of competition theory view competition from the perspective of the Lotka-Volterra model. The appeal of the logistic model to ecology today has partly resulted from interesting interactions among early twentieth century ecologists who passed on an academic tradition to ecologists in the 1950's and 1960's (Kingsland 1982), however, it is also conceptually simple. To apply the logistic model to real species assemblages, however, at least two assumptions about the species assemblages are needed. The first is that the resources available to the species are limited. Here resources are most commonly assumed to be food resources, and thus the competitive mechanism is exploitation. However, if the resource being considered is space, then interference might be envisioned as the mechanism of competition. A second assumption is that the population densities of the species are near equilibrium (i.e., $N_i \cong K_i$). These two assumptions ensure that changes in population densities of the species will be dominated by the competition coefficients. To see this, assume in the logistic equation for species i

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i}\left(K_i - N_i - \sum_{j \neq i} \alpha_{ji} N_j\right),$$

that $N_i \cong K_i$, then $N_i/K_i \cong 1$ and $K_i - N_i \cong 0$, so

$$\frac{dN_i}{dt} \cong -r_i \sum_{j \neq i} \alpha_{ji} N_j.$$

One major result that follows from the Lotka-Volterra equations is that when resources (however defined) are abundant, species carrying capacities (K_i) are much larger than their population sizes, and hence the term $(-N_i - \sum_{j \neq i} \alpha_{ji} N_j)$ is small compared to K_i. In such situations the effects of competition are thought to be relaxed (Fretwell 1972).

It is obvious from an examination of Wiens' (1977) criticisms of competition theory that he envisioned essentially the same type of competitive model as suggested above. His ecological crunch model rested on the assumption that as resources become more abundant competition relaxes and coexistence of species is facilitated, which is essentially an extension of Fretwell's (1972) analysis to include seasons in which resource abundance varies widely.

INTERFERENCE AND EXPLOITATIVE COMPETITION

In his discussion of the mechanisms of competition, Schoener (1983) subdivided the two general categories of exploitation and interference into several categories. His first category, termed "consumptive" competition, refers to what most researchers generally term exploitative competition. This process involves removal of resources by one species leaving less for competing species. Schoener (1983) divided interference competition into a number of categories, three of which are applicable to avian species. The first type, which he termed "preemptive" occurs when an individual occupies a unit of space in which some needed resource exists, and simply by its presence interferes with the ability of another individual of a competing species to use the resource contained in that space. Schoener (1983) pointed out that this primarily involved sessile organisms, but this type of competition may also apply to organisms which require a fixed unit space, e.g., nest-sites in birds. In the discussion below, this type of competition will not be considered. The second type of interference which Schoener (1983) recognized was termed "territorial" competition, a process whereby an individual of a competing species aggressively defends a unit of space in some manner against individuals of another species. Finally, Schoener (1983) recognized that mobile individuals of different species, while in the course of their movements in a habitat, might cause some sort of stress or injury on each other. He termed this type of competition "encounter" competition. Encounter competition may occur as an active behavioral adjustment by individuals of competing species to prevent resource acquisition or population growth of competitors, leading

to reduced resource intake or loss of individuals. This type of interference may be termed active interference. Encounter competition as Schoener (1983) defined it may also occur as the consequence of nonaggressive behaviors. This type of interference competition might be termed passive interference. Charnov et al. (1976) first recognized that this type of interference might be important in structuring communities. They suggested that the foraging activities of some species which consume mobile prey might result in movements of prey into "refugia" where they are unavailable to competitors. Hence, resources would be temporarily depressed, rather than depleted as might occur from consumptive competition. Passive interference might also occur between individuals of different species whose foraging paths cross close enough in space and time so that the foraging activities of one or both individuals is impeded or prevented exclusive of any antagonistic responses.

Exploitation and interference competition are likely to be prominent in different ecological settings. Active forms of interference necessarily carry with them costs (Case and Gilpin 1974, Schoener 1976) which place constraints on the abilities of species to actively interfere. Hence, resources must be abundant enough to offset the costs of active interference. Morse (1980a) also points out that resources should be predictable in space and time in order for interference to confer benefits on individuals. Passive interference, on the other hand, is likely to occur any time resources become concentrated. Birds often respond to increased productivity by increasing population densities (Dunning and Brown 1982). Increased population densities should lead to greater likelihood of individuals of competing species encountering each other and thus increase the frequency of passive interference events.

Based on these ideas a tentative model of the ecological settings in which each type of competition should occur can be constructed (Table 1). The applicability of this model is based on the assumption that resources (however defined) are the primary factors to which the species respond on an evolutionary time scale. Hence, if patterns in the physical environment that are independent of resource characteristics (e.g., temperature as it effects thermoregulation) are more important than resources in shaping the species' behavior, then the model discussed below may only poorly fit the actual behavior of the species. Species should respond to three characteristics of resources. First, resource density should affect competitive behavior between species since active interference has costs in terms of energy expenditure associated with it. It is assumed that an individual cannot gather resources and actively interfere with another individual at the same time, hence active interference is more likely to occur when an individual can quickly replenish its energy stores. Second,

TABLE 1

TYPES OF INTERSPECIFIC COMPETITION WHICH MAY BE OBSERVED IN DIFFERENT ECOLOGICAL SETTINGS; THE ENTRIES ARE THE TYPE OF COMPETITION MOST LIKELY TO BE ASSOCIATED WITH THE ECOLOGICAL SETTING DESCRIBED

Resource density	Resource dispersion	Temporal patterns of resource abundance	
		Predictable	Unpredictable
Abundant	Concentrated	Active and passive interference, territoriality	Passive interference, facultative active interference
Abundant	Dispersed	Passive interference facultative active interference	Exploitation
Rare	Concentrated	Active and passive interference, territoriality (rarely)	Passive interference, facultative active interference
Rare	Dispersed	Exploitation	Exploitation

the spatial patterning of resources should influence the ability of species to defend resources successfully. Resources which are concentrated in small areas require less energy expenditure to defend, and hence are more likely to allow species to maintain small enough cost-benefit ratios to make active interference feasible. Finally, the temporal patterning of resource abundance should influence the ability of species to develop resource defense systems. If resources are highly stochastic in their appearance, then individuals should not be able to gain enough benefit on a regular basis to allow them to be successful at resource defense (Morse 1980a). On the other hand, resources that are regular on an ecological time scale should be used by more species than those that are sporadic, hence increasing opportunities for individuals to develop behavioral mechanisms of dealing with interspecific competitors. It should be obvious that these three characteristics of resources interact and provide a number of different ecological settings in which interspecific competitive mechanisms might evolve (Table 1).

When resources are abundant, concentrated and predictable active interference is feasible (Table 1) since individuals can expend relatively little energy on resource defense and rapidly obtain necessary energy to replace energy spent. In such an ecological setting, it would be advantageous for species to develop territorial or hierarchical systems whereby interspecific contests are settled quickly with a minimum of energy expenditure. However, when resources are abundant and concentrated, but

appear sporadically and unpredictably, the benefits an organism may derive from them may not be regular enough over time to allow species to invest the energy necessary to maintain resource defense. In such a setting, during periods of irregular resource abundance, individuals might benefit from maintaining a behavioral flexibility (facultative active interference in Table 1) enabling them to actively interfere during times of resource abundance, and cease interference during times of resource rarity. If resources are abundant, and predictable, yet dispersed enough so that energy costs for defending more than a single resource unit are high, then again it would be advantageous for an individual to actively interfere with another only sporadically. In such a setting, passive interference events might occur on a regular basis since densities would be high. If resources are abundant and dispersed, but unpredictable, then densities of consumers might remain low during irregular resource pulses, and consumptive competition might exist only during the periods of low resource density (see below).

When resources are rare, it will be more difficult for individuals to invest in behaviors which involve elaborate energy expenditures, hence active interference may be less prevalent in habitats with scarce resources than in habitats with resource abundance. When resources are concentrated in such habitats, the resulting ecological conditions might give rise to qualitatively similar patterns of interspecific competitive mechanisms to those found when resources are abundant, but less expensive forms of interference might be expected and interspecific territoriality should be relatively rare. When resources are rare and dispersed, then individuals might only be able to expend energy on resource acquisition (e.g., foraging). Hence the only way species might compete in such situations might be to remove the already limited supply of resources from the area of joint occupancy of two competing species.

It should be realized that testing the predictions of the model described above might be very difficult. While the model has been constructed in a dichotomous fashion, terms such as "rare" and "abundant" are likely to represent extremes along a continuum of resource abundances. To test even the qualitative predictions of the model it would be necessary to generate more precise definitions of the nature of resource density, dispersion, and temporal patterning based on a specific system. Another complicating factor is that environments in which species exist are not constant but usually change in a cyclic or stochastic manner. Hence, at a given time, a habitat might present a setting in which resources are abundant, concentrated, and predictable and later that same habitat might have rare resources that are dispersed and unpredictable. In the following section, I review a number of studies that deal with avian competition in

the context of the model presented above, however, the level of rigor of these studies does not allow a rigorous evaluation of the usefulness of the model in predicting the types of competitive interactions that species might experience.

COMPETITION IN BIRD COMMUNITIES

What is the prevalence of interference and exploitation in bird communities and to what extent do they shape ecological relationships among bird species? To adequately answer these questions one would need a large number of studies on many species assemblages done at a level of rigor sufficient to differentiate among the intensity of the types of competition envisioned in the model discussed in the preceding section. Such a sample is probably impossible to obtain, however, a number of studies have been done which provide at least a rough idea of the nature and prevalence of the several types of competition in real ecosystems.

Some studies have suggested that since aggressive encounters were infrequently observed among species, the major mode of the presumed competition among the species studied was exploitation (Noon 1981, Rusterholz 1981). From the preceding discussion, however, it follows that absence of active interference events does not indicate absence of all interference interactions. At this time it is extremely difficult to document the presence and frequency of passive interference events. Such events are very likely to go undetected by human observers because they do not create sufficient auditory or visual cues to attract attention.

Because the mechanism of exploitation depends on the ability of one species to reduce prey numbers to a level that would have a significant impact on the population growth rate of other species, studies which demonstrate a drop in prey numbers attributable to avian predation are extremely important in assessing the probability of exploitation being an important factor influencing bird communities. A number of studies have provided both direct and indirect evidence for the ability of birds to reduce prey numbers. Both Solomon and Glen (1979) and Holmes et al. (1979) performed experiments in which avian predators were prevented from removing prey in certain areas. Both studies demonstrated a measurable increase in prey in areas not available to avian predators. Recently, E. O. Garton (pers. comm.) has found similar results for birds preying on the western spruce budworm (*Choristoneura fumiferana*). Gunnarson (1983) showed that overwinter mortality of spiders living in spruce trees was lower on branches on which netting had been used to prevent avian predation. Similar results were obtained by Askenmo et al. (1977) in another investigation of the impact of wintering birds on spiders in spruce forests. Hence, experimental evidence suggests that avian predation can

cause significant reductions in arthropod densities during both the breeding and nonbreeding seasons. In a slightly different vein Gill and Wolf (1979) showed that sunbirds (*Nectarinia* spp.) could remove significant amounts of nectar potentially available to other species.

A number of studies have provided indirect support of the role of avian predators in reducing population densities of their prey. Gibb (1954) noted that Great Tits (*Parus major*) apparently reduced insect larvae to a certain specific level before moving to feed elsewhere. Peterman et al. (1979) reviewed studies on the eastern spruce budworm which suggested that avian predators played an important part in damping budworm irruptions. Similar evidence along these lines was reviewed by Otvos (1979). Heinrich (1979) discovered that lepidopteran larvae palatable to birds tended to forage in a manner which minimized the visual impact of their foraging activities. Many of these larvae are also cryptically colored, suggesting that predators which use visual clues while hunting have been important in shaping their phenotypic characteristics.

Although evidence suggests that there is certainly potential for exploitative competition in many avian communities, most studies have failed to demonstrate that avian species could remove enough prey to affect the growth rate of other species (Maurer 1983a). This is critical information because it is possible that measurable reductions in food supply may not be sufficient to reduce the effective food supply available to a second species (Maurer 1983b). Reduced resources is a necessary, but not a sufficient condition for the occurrence of exploitative competition. Minot (1981) removed Blue Tit (*Parus caeruleus*) broods from an oak wood in England and learned that nestling weights of Great Tits were higher in the experimental area than in a control area. Since weight of nestlings is related to survival probability (Perrins 1965) this implies that Blue Tits were able to remove enough insect larvae for their broods to affect the demographics of Great Tits. In this situation, it is difficult to objectively determine the characteristics of the resources available to tits during the breeding season. It is likely that they are abundant relative to winter food availability (Gibb 1960). The insect prey of tits may be relatively evenly dispersed (Tinbergen 1960), and apparently appear at widely differing times from year to year (Tinbergen 1960, Perrins 1965). Hence, food for tits during the breeding season may be abundant, dispersed, and unpredictable.

Abundant evidence exists for the prevalence of active interference, though this may be due to the relative ease with which these types of interactions may be observed. Williams and Batzli (1979a, b) found that the presence of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) influenced the distribution and foraging behavior of other bark foraging

birds during winter in central Illinois. These interactions between *M. erythrocephalus* and other bark foragers apparently relaxed during the breeding season, a time when resources presumably would be more abundant. During the winter, however, the primary foods of these species may be concentrated enough to increase the frequency of interspecific encounters over that encountered during the breeding season. Williams and Batzli (1979b) commented that the majority of aggressive encounters occurred in fall, when Red-headed Woodpeckers were establishing winter territories. Interspecific territoriality during the breeding season has been documented for a number of passerine birds (Orians and Willson 1964), including Palearctic sylviine warblers (*Sylvia* spp.) (Cody and Walter 1976, Cody 1978, Garcia 1983); (*Phylloscopus* spp.) (Saether 1983a, b) and vireos (*Vireo* spp.) (Rice 1978, Robinson 1981).

Aggressive encounters among species are not necessarily territorial conflicts (Davies 1978). Edington and Edington (1983) described several instances of active interference among West African birds. They found that in interactions among several species of sunbirds, species dominant in aggressive encounters were those for which the interaction took place in a favored feeding zone. Edington and Edington (1983) found a similar type of interaction occurred between White-throated Bee-eaters (*Merops albicollis*) and Ethiopian Swallows (*Hirundo aethiopica*). Sherry (1979) found that American Redstarts (*Setophaga ruticilla*) and Least Flycatchers (*Empidonax minimus*) interacted aggressively during the breeding season in New Hampshire although their breeding territories overlapped extensively. Morse (1976) showed that during the breeding season wood warblers (*Dendroica* spp.) in spruce forests were interspecifically aggressive, and that encounters were usually more frequent later in the season when feeding of nestlings by parents might result in many interference events during foraging. These encounters apparently did not lead to interspecific territoriality.

In assemblages of nectar-feeding birds, interesting comparisons can be made between the frequency of interference events and the qualitative predictions of the model discussed above, since the dispersion and density of the resources (nectar) can easily be measured and compared to interference behaviors. Carpenter (1978) summarized results from several nectarivore communities she studied. In a community of Hawaiian drapanidines, Carpenter (1978) showed that during a year of overall depressed nectar availability, aggression among three species of honeycreepers was increased. In the year of depressed nectar availability, flowers produced the same amount of nectar but were depleted quickly. However, flowers were concentrated in one portion of the canopy during the poor year, while they were dispersed during two favorable years. In the poor year,

all three honeycreeper species attempted to forage in the same area. The dominant species was able to defend territories in the densest flower clumps, and nectar availability in these clumps was in excess of the species requirements for maintenance. Nectar production was apparently relatively predictable within a given year, but during good years was abundant and dispersed, hence leading to few opportunities for interference. During the bad year, nectar was generally rare, but concentrated, which led to a concentration of consumers. This in turn made it necessary for two of the honeycreepers to become territorial, for otherwise they could not adequately meet their energy requirements (Carpenter 1978:810).

In a community of Australian honeyeaters (Melaphagidae), Carpenter (1978) noted that nectar was extremely abundant and that the honeyeaters in that community were not aggressive. Apparently, nectar producing flowers were not concentrated enough relative to their abundance to necessitate aggression, though aggression among honeyeaters has been reported. These species of honeyeaters, however, relied heavily on insect densities, hence the importance of nectar to their behavior is questionable. Dow (1977) showed that another melaphagid excluded all other bird species from habitat near colonies. This species was more successful in driving out other species in structurally simple habitats, where food resources could be expected to be concentrated relative to habitats with many vegetation layers.

Pimm (1978) performed an experiment with hummingbirds at feeders at which he varied the predictability of resources while keeping their density and dispersion constant. He calculated two measures of competition, one which he termed exploitation, the other which he termed interference. However, resource abundance remained constant in the experiment, and the measure of exploitation, a regression coefficient of the time that one species spent at each feeder vs the time that other species spent at each feeder (feeders were replications) was actually a measure of passive interference, since feeders were constantly replenished. His interference measure was a regression coefficient of feeder use by one species vs time spent in feeder defense in a second species, which is a measure of active interference. His results are consistent with the model presented above: a decrease in resource predictability significantly decreased both passive and active interference.

IMPLICATIONS FOR COMPETITION THEORY

Many discussions of competition implicitly assume that the effects of the different types of competition tend to produce similar results (e.g., Miller 1967). Thus, "niche partitioning," the differential use of resources by species, is assumed to have been the result of competition for limiting

resources (e.g., MacArthur 1958, Morse 1980b, Noon 1981, Alatalo 1982) regardless of the type of competition involved. This assumption is also implicit in Wiens' (1977) criticisms of competition theory. He listed several assumptions made by competition theorists in applying the theory to natural systems, many of which are artifacts of the Lotka-Volterra paradigm. For example, the assumption that resources are limiting is crucial to Lotka-Volterra competition. Wiens (1977) pointed out that very often species may exist in environments which are seasonally highly productive, and hence species densities would be far below environmental carrying capacity as envisioned in the Lotka-Volterra model (see also Fretwell 1972). Wiens (1977) assumed that in these situations, competition would generally be relaxed. However, the model presented in the present paper suggests that when resources are abundant, although exploitation is relaxed, interference may increase, especially if resource abundance is concentrated, or if species are able to respond to increased resource abundance by increasing their densities.

Some models of interference and exploitative competition have suggested that at high resource levels interference should be minimal and should increase when resources become scarce (Gill 1974, Carpenter and MacMillen 1976, Wolf 1978). However, few of these models have differentiated between resource abundance and resource dispersion. If resources become concentrated during periods of low resource levels, then interference is likely to increase because individuals must search for and secure resources in a much smaller area, hence increasing the rate of encounters with other individuals while at the same time removing a greater proportion of the resources. At high resource densities, if resources are generally dispersed then the opportunities for interference might be relaxed. The utility of the model discussed in this paper is that it considers not only variation in resource abundance, but also the spatial and temporal patterns of resource availability that may influence competitive relationships. In doing so it generalizes the model of Orians and Willson (1964), who suggested that interspecific territoriality should be more prevalent in structurally simple habitats. They felt that interspecific territoriality in such habitats should increase because fewer niches are available. The model I have presented suggests that if fewer niches exist in simple habitats, it is because resources are spatially compressed or concentrated.

Just as exploitative and interference competition might be expected in different ecological settings, the evolutionary results of these types of competition might be expected to be different. If it is assumed that reduction in competition will increase an individual's fitness, then it follows that species should evolve to reduce competition. Selection to reduce interference competition should involve different phenotypic traits than

those that are involved in exploitative competition. When the latter type of competition is occurring, resources may often be dispersed so as to be non-defendable (Table 1). If resources are rare enough, then individuals which avoid areas containing resources may be selected against. If at the same time densities of competitors are low, and hence interspecific encounter rates low, then it would be most advantageous for an individual to use all areas within its foraging range. Selection might operate in this situation to cause species to diverge in the types of resources taken so species would use different types of resources, but use all available resource patches. On the other hand, the avoidance of individuals which are likely to actively or passively interfere would reduce interference competition. Such interference would be reduced if different species used spatially (or temporally) different parts of the habitat. Hence, exploitation should generally lead to niche partitioning via reduced resource overlap while interference should lead to niche partitioning via reduced spatial overlap. For example, differences in prey size used may result from exploitation, while differences in foraging zones may result from interference.

Although the two types of competition may have different evolutionary consequences, it is likely that species evolve in highly complex environments in which both types of competition may be experienced along with numerous other factors affecting individual fitness. Hence the phenotypic results of the two types of competition may be difficult to distinguish from those produced by other selective pressures. As an example, Blue and Great tits compete for nest holes by interference (Alatalo 1982) and also have been shown to compete exploitatively for food for nestlings (Minot 1981, Alatalo 1982). The result of this array of selection pressures is that species might be constrained in their abilities to evolve to alleviate competitive pressures (Maurer, unpubl.). Though we may be able to understand general relationships among competitive pressures and niche characteristics, assigning specific selection pressures (e.g., exploitation or interference) to specific phenotypic characteristics (e.g., specific niche differences) may, in practice, be an exercise in futility because cause-effect relationships may be impossible to verify, even indirectly (Wiens and Rotenberry 1981b, Wiens 1982). Competition, whether exploitative or interference, is likely to be one of many factors which together operate on avian assemblages to shape the composition and densities of the species which comprise them.

SUMMARY

Two types of competitive interactions occur among species in bird communities: exploitation and interference. Most theoretical and empirical approaches to the ecology of competition have assumed the evolutionary and ecological results of these two processes are the

same. Interference can be active, a result of direct behavioral interactions which carry with them a cost, or passive, the indirect result of other activities of competitors (such as food gathering). A model is presented which suggests the type of ecological settings in which the various types of competition can occur. Generally, the model suggests that as resources become less abundant, more widely dispersed, and less predictable, exploitation should become more prevalent while interference should become less prevalent.

Research on birds indicates that active interference is very common, however, exploitation and passive interference, if prevalent, may be difficult to document. Discussions of the prevalence of competition have centered on the Lotka-Volterra conceptualization of competition. However, if interference is common when resources are abundant, then resource limitation may not be a prerequisite of niche divergence. Exploitation should lead to niche partitioning via reduced resource overlap, while interference should lead to niche partitioning via reduced spatial overlap. However, both of these factors may act as selection pressures on competing species in addition to many other selection pressures, hence the ability of species to respond to selection to reduce competition might be greatly modified or inhibited.

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NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society announces the second annual grants-in-aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia*. Presently three annual grants of single or multiple awards totalling $3,000.00 are awarded and include:

Bluebird Research Grant—Available to student, professional or individual researchers for a suitable research project focused on any of the three species of bluebird from the genus *Sialia*.

General Research Grant—Available to student, professional and individual researchers for a suitable research project focused on a North American cavity nesting species.

Student Research Grant—Available to full-time college or university students for a suitable research project focused on a North American cavity nesting species.

Further guidelines and application materials are available upon request from **Theodore W. Gutzke,** Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746. **Completed applications must be received by 31 January 1985; decisions will be announced by 15 March 1985.**

Wilson Bull., 96(3), 1984, pp. 396–407

VISUAL DISPLAYS AND THEIR CONTEXT IN THE PAINTED BUNTING

Scott M. Lanyon and Charles F. Thompson

The 12 species in the bunting genus *Passerina* have proved to be a popular source of material for studies of vocalizations (Rice and Thompson 1968; Thompson 1968, 1970, 1972; Shiovitz and Thompson 1970; Forsythe 1974; Payne 1982), migration (Emlen 1967a, b; Emlen et al. 1976), systematics (Sibley and Short 1959; Emlen et al. 1975), and mating systems (Carey and Nolan 1979, Carey 1982). Despite this interest, few detailed descriptions of the behavior of any member of this genus have been published. In this paper we describe aspects of courtship and territorial behavior of the Painted Bunting (*Passerina ciris*).

STUDY AREA AND METHODS

The study was conducted on St. Catherines Island, a barrier island approximately 50 km south of Savannah, Georgia. The 90-ha study area ("Briar Field" Thomas et al. [1978: Fig. 4]) on the western side of the island borders extensive salt marshes dominated by cordgrasses (*Spartina* spp.). The tract's evergreen oak forest (Braun 1964:303) consists primarily of oaks (*Quercus* spp.) and pines (*Pinus* spp.), with scattered hickories (*Carya* spp.) and palmettos (*Sabal* spp. and *Serenoe repens*) also present. Undergrowth was scanty so that buntings were readily visible when on the ground.

As part of a study of mating systems, more than 1800 h were devoted to watching buntings during daily fieldwork in the 1976–1979 breeding seasons. In 1976 and 1977 observations commenced the third week of May, after breeding had begun, and continued until breeding ended in early August. In 1978 and 1979 observations began in April, several days before the first buntings returned to the study area, and continued until nesting activities ceased in 1978 but only until mid-July in 1979, about 2 weeks before breeding ended.

Adult buntings were mist-netted and banded with a unique combination of aluminum U.S. Fish and Wildlife Service band and three plastic colorbands (two bands/leg). In addition we applied paint (Testor's airplane dope) to either the outer primaries of one wing or the outer rectrices of selected individuals to facilitate identification in the field.

We attempted to visit each part of the study area daily and to observe every resident bunting. Whenever an individual was sighted, its identity, type of activity, location, and the time of day were recorded either on a

TABLE 1
CLASSIFICATION AND DESCRIPTION OF CONTEXTS IN WHICH MALES PERFORMED PARTICULAR BEHAVIORS

Context number	Description of context
I	Unknown; no other bunting present
II	With female that is not its mate
III	With mate
IV	With own mate and neighboring male
V	With neighboring male and its mate
VI	With neighboring male
VII	With fledgling
VIII	Response to playback of species' song
IX	With unidentified greenish yellow-plumaged bunting (unbanded female or yearling male)

tape recorder for later transcription or in field notebooks. Each bunting was followed and its behavior noted until the bird was lost from sight. The location of each sighting was determined with respect to rows of marked stakes placed 20 m apart in a grid covering the study tract. Additional observations were made on buntings attracted to a model of a male bunting placed near a recorder playing tape recordings of the species' song. These responses were filmed with a Super-8 movie camera. Drawings of bunting postures were made from written descriptions and films.

RESULTS

Behavior.—The following descriptions are based on the most frequently observed patterns. The context in which each behavior occurred in males was classified into one of nine categories to simplify presentation and analysis (Table 1). When males were not performing one of the seven displays described in this paper, their behavioral category is classified as "other" in Table 2. This category includes foraging, singing, and maintenance activity. The frequency of "other" behaviors in each of the nine social contexts is used as an estimate of the frequency that buntings experienced these contexts.

(1) Upright: The male hops on fully extended legs with tail raised 45–90° above the body's axis, head extended and slightly raised, and feathers appressed. The wing tips are held below the tail, exposing the red rump (Fig. 1a). This is usually performed on the ground. Fifty-three percent of the uprights were performed in the presence of a female other than the male's mate (context II) or in the presence of a neighboring pair (context

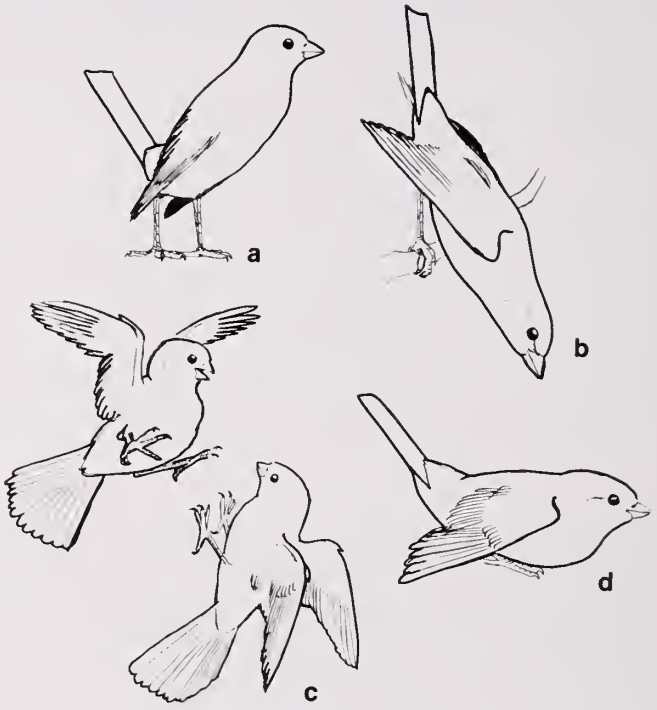

FIG. 1. Painted Bunting displays and postures: (a) Upright, (b) Bow, (c) Flutter-up, (d) Wing Quiver (see text).

V) (Table 2). The number of uprights given in contexts II and V was significantly greater than the number of observations of "other" behaviors in the same contexts ($\chi^2 = 209.9$, df = 1, $P < 0.001$; $\chi^2 = 13.2$, df = 1, $P < 0.001$, respectively). Uprights often occur when two males encounter each other at the perimeters of their territories. In such cases, the males maintain a separation of <1 m as they hop parallel to one another for several meters in the upright posture.

(2) Bow: Bows are performed from perches, at or above the level of the bunting toward which they are directed. The long axis of the body is rotated so that the tail is raised and the head lowered toward the other bird (Fig. 1b). If the bunting is clinging to a vertical perch, such as a cordgrass stem, the long axis of the body and tail is often perpendicular to the ground; if, however, the perch is horizontal, the axis seldom exceeds a 45° angle with the ground. The wing tips are extended from the body and lowered, thereby exposing the rump. Bows occurred significantly more frequently than "other" behaviors in the presence of a female that was

TABLE 2

FREQUENCY OF MALE VISUAL DISPLAYS IN VARIOUS SOCIAL CONTEXTS

Behavior	N	Context[a]									χ^{2b}
		I	II	III	IV	V	VI	VII	VIII	IX	
Bow	104	8.7[c]	13.5	14.4	17.3	29.8	8.7	2.9	1.9	7.7	50.9
Upright	70	11.4	40.0	10.0	8.6	12.9	10.0	1.4	0.0	5.7	236.9
Wing quiver	43	16.3	0.0	2.3	2.3	7.0	37.2	2.3	27.9	4.7	1907.1
Butterfly flight	33	3.0	3.0	6.1	27.3	18.2	39.4	3.0	0.0	0.0	84.8
Moth flight	11	18.2	9.1	18.2	0.0	18.2	0.0	0.0	27.3	9.1	—
Flutter-up	69	—	0.0	0.0	36.2	36.2	26.1	1.4	—	2.9	77.4
Feather pulling	8	0.0	50.0	12.5	12.5	25.0	0.0	0.0	—	0.0	—
Courtship	19	5.3	57.9	26.3	0.0	0.0	0.0	0.0	0.0	10.5	—
Other	4286	51.1	3.9	15.2	4.5	4.1	13.1	3.1	0.2	4.9	—
Total N	4643	2217	226	686	252	252	623	141	24	229	—

[a] See Table 1.

[b] To minimize false positives (Type I errors), the distribution of observations for each behavior (if N > 15) was compared across contexts with that of Other behavior by employing a 2 × 9 contingency χ^2 test. The calculated χ^2 values given in the last column are significant at $P < 0.05$, so χ^2 tests for each behavior (if N > 5) compared with Other behavior in each context were performed and the results reported in the text.

[c] Values are percentages of row totals.

not the male's mate (context II, $\chi^2 = 23.5$, df = 1, $P < 0.001$), with the male's mate and a neighboring male (context IV, $\chi^2 = 36.7$, df = 1, $P < 0.001$), and with a neighboring male and its mate (context V, $\chi^2 = 151.2$, df = 1, $P < 0.001$) (Table 2). Bows are initiated whenever the bunting toward which the bow is directed moves, or when the bowing male itself moves to a new location during an encounter. In the latter case, the bow is given immediately upon landing on the new perch.

(3) Flutter-up: Flutter-ups begin when one male flies toward another approaching male. Both decelerate and extend their feet forward. With an audible beating of wings and with grappling feet, they ascend as high as 5 m (Fig. 1c). Flutter-ups typically end when the still-grappling males drop to the ground, disengage, and fly in opposite directions or sit quietly near each other. Occasionally, one of the males succeeds in gaining the superior position as they ascend, in which case the lower male attempts to disengage itself before they fall to the ground. Usually only one flutter-up occurs during an encounter. Flutter-ups occurred significantly more frequently than "other" behaviors when a pair approached a lone neighboring male (context IV, $\chi^2 = 54.0$, df = 1, $P < 0.001$) or a neighboring male accompanied by its mate (context V, $\chi^2 = 62.2$, df = 1, $P < 0.001$) (Table 2).

(4) Wing quiver: Wing quivers usually occur after a male has landed on the ground or on a perch and is facing another bunting of either sex. The crouching male erects its body feathers, lifts the wings, lowers the wing tips, and raises its tail to about 45° above the body's long axis (Fig. 1d). The lowered wings are rapidly quivered. Occasionally the wings are extended and raised above the back and rapidly quivered (as in Fig. 2c). Wing quivers end with the non-displaying male's flying off alone or being chased by the displaying male. Wing quivers occurred significantly more frequently than "other" behaviors when a male responded to a model of a male and song playback (context VIII, $\chi^2 = 749.9$, df = 1, $P < 0.001$) and when neighboring males encountered each other (context VI, $\chi^2 = 21.5$, df = 1, $P < 0.001$), especially when a male on its own territory was responding to another male's singing nearby (Table 2).

(5) Butterfly flight: Butterfly flights are characterized by slow, deep wing beats and undulating flight. During butterfly flights the body feathers appear to be appressed. Butterfly flights are directed toward a stationary bird or occur when a retreating bunting is being followed. Of 33 butterfly flights, 28 (85%) occurred during interactions between males (contexts IV, V, VI) and for each of these contexts butterfly flights occurred significantly more frequently than "other" behaviors ($\chi^2 = 38.3$, df = 1, $P < 0.001$; $\chi^2 = 16.4$, df = 1, $P < 0.001$; $\chi^2 = 19.7$, df = 1, $P < 0.001$, respectively) (Table 2).

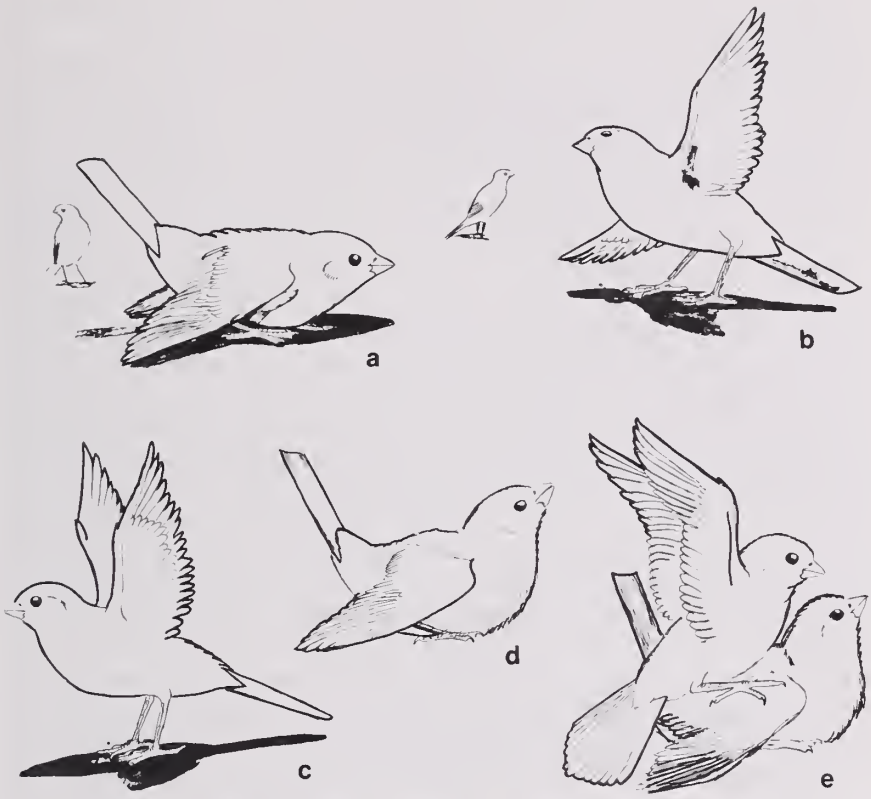

FIG. 2. Courtship sequence (a–c), solicitation (d), and copulation (e) of the Painted Bunting (see text).

(6) Moth flight: In moth flight the body feathers are erected and the extended wings are rapidly fluttered. These shallow wing beats produce a slow, descending flight. Moth flights occur when a male flies during wing quivers.

(7) Feather pulling: Feather pulling occurs after a male dives upon and hits a flying female, driving her to the ground. The male stands upon the crouching female's back, takes one or more of the female's remiges or rectrices in his bill, and appears to pull with a steady pressure for several seconds before flying off. During feather pulling the female remains motionless and sometimes gives soft call notes. Seven of the eight feather pulls involved a female other than the male's mate (Table 2).

Courtship and copulation.—The sequence of displays and postures in-

volved in the establishment or maintenance of a pair-bond are described in this section.

(1) Typical sequence: The male in moth flight glides to an open area of ground 1–2 m from the female. Facing away from the female, the male wing quivers (Fig. 2a). The female hops toward the male, which responds by walking (not hopping) away. The intensity of the male's wing quivers increases at this point and his breast touches the ground. After the female stops, the male turns toward her and straightens his legs. The rate of the wing quivers increases and the wings are gradually and alternately raised to a fully extended position above the back as the male turns toward the female (Fig. 2b). As one wing is raised, the other is extended slightly downward. The male then walks toward the female with both of his wings held rigidly above the back (Fig. 2c). When within 1 m of the female, the male flies to the female and hovers over her using rapid, shallow wing beats, as in moth flight. Either copulation follows (see below) or the female crouches with appressed body feathers and opens her bill while facing the male. If the male tries to mount, either copulation occurs or the female lunges at the male and drives him off. In the latter case, the male often lands nearby and crouches facing away from the female. The male may then begin walking away from the female and repeat the courtship sequence.

(2) Copulation: During copulation the female crouches, erects body feathers, raises tail and head, and lowers her wings (Fig. 2d) as the male hovers, turns in mid-air, and lands on her back (Fig. 2e). The male perches on the female's back, using his wings to maintain balance as his cloaca is brought into contact with the female's cloaca. After 5 sec or less the male dismounts, faces away from the female, and crouches with breast touching the ground, wings drooped, and tail raised. The female remains at the site of copulation and ruffles her feathers vigorously for several seconds. The erection of the contour feathers and the shaking of the body appear more pronounced than are similar movements made during preening.

(3) Contexts: Courtship sequences were observed 19 times, of which 11 (59%) occurred in context II and 5 (26%) in context III. The courtship sequence is not a prerequisite for the occurrence of copulation; females frequently assumed the crouched posture (Fig. 2d) in the presence of males that had not displayed. Copulations not preceded by the courtship sequence occurred in a variety of contexts (Table 3).

Nest-site exploration.—Of 35 observations of nest-site exploration, 32 (91%) involved both members of the pair; the remaining three cases involved only the female. Both birds search the foliage, much as they do when foraging, except that the search is characteristically more rapid and

TABLE 3
CONTEXTS IN WHICH FEMALES CROUCHED IN SOLICITATION POSTURE, 1978 AND 1979 ONLY

	Soliciting female with:					
	Mate	Mate and male	Mate and another pair	Non-mate male	Mate and female	Total
Number	24	11	7	2	1	45
Percent	53.3	24.4	15.6	4.4	2.2	100

no food is taken. The male or female enters clumps of spanish moss (*Tillandsia usneoides*) or other dense vegetation, where it crouches motionlessly. The crouching female, but never the male, frequently arranges foliage around itself. In 12 of 32 cases (37%) involving pairs, the male preceded the female in entering clumps of foliage, thereby appearing to lead the female to potential nest-sites. In one instance, a yearling male perched in a potential nest-site and was mounted several times by its mate (Thompson and Lanyon 1979).

Male parental care.—Males never fed nestlings, but they did defend nests. Males frequently gave loud calls as they followed potential avian predators (Blue Jays [*Cyanocitta cristata*] and grackles [*Quiscalus* spp.]) through the canopy until the predator had left the vicinity of the nest. The only male that entered its own nest did so when Blue Jays were near the nest clump. Several males fed fledglings, but most did not; of 41 broods that produced at least one fledgling, only nine (22%) had fledglings that were fed by the male.

DISCUSSION

The design of this study does not permit detailed discussion of the motivational states underlying the described behaviors. However, some information on the state of displaying individuals is provided by the contextual analysis. In the following discussion we use this contextual information to suggest functions for these displays as well as to compare the form and context of the visual displays of the Painted Bunting with similar displays in related passerines.

Dorsey (1976) reported a display, similar to the Painted Bunting's upright, in Bachman's Sparrow (*Aimophila aestivalis*). In both species the display is performed in a context of potential aggression or danger to the individual. The bunting's upright is similar to the Common Chaffinch's (*Fringilla coelebs*) head-up display, which Marler (1956:62) assigned an intermediate position on a continuum between attack and escape behaviors.

The bow display of the Painted Bunting does not occur in Indigo Buntings (*P. cyanea*) or Lazuli Buntings (*P. amoena*). Instead, in a similar social context, Indigo Buntings rotate the body slowly through an arc from side-to-side and Lazuli Buntings remain motionless; neither lowers the head below the horizontal (Thompson 1965). The head-forward display of many emberizids and fringillids (Hinde 1955, Dilger 1960, Thompson 1960, Andrew 1961, Coutlee 1967, Samson 1977) shares some similarities with the Painted Bunting's bow. The head-forward and bow displays are likely homologous, as they occur in similar social contexts. The bow display probably serves as a low-intensity threat, as has been suggested for the head-forward display (Hinde 1955). A display similar in form to that of the bow of the Painted Bunting has been described in the Hawfinch (*Coccothraustes coccothraustes*) (Hinde 1955); however, although the head is lowered, Hawfinches also erect their contour feathers, which Painted Buntings do not do. Hinde (1955) suggested that the display communicated the submissive status of the displaying bird.

The wing quiver display has been described in Painted Buntings (Parmalee 1959, Thompson 1965, this study) and Indigo Buntings (Thompson 1965, Emlen 1972), but not in Lazuli Buntings (Thompson 1965). A similar display has been reported in Grasshopper Sparrows (*Ammodramus savannarum*) (Bent 1968). The Song Sparrow's (*Melospiza melodia*) puff-sing-wave differs from the wing quivers of the Painted Bunting in that the tail is not raised above the horizontal (Nice 1943). Wing quivers function as high intensity threat displays.

Indigo and Lazuli buntings regularly engage in flutter-ups (Emlen et al. 1975), as do many emberizines (Sabine 1952, Bent 1968). In Painted Buntings flutter-ups usually occurred at the conclusion of a series of encounters between males that were defending space or mates.

Thompson (1965) describes a fluttering flight (our moth flight) in the Painted Bunting as similar to the flight song of the Indigo Bunting (see, also, Thompson 1972), except that in the Painted Bunting no song is given. M. Carey (pers. comm.) frequently observed a fluttering flight in the Indigo Bunting that was often performed without song during territorial encounters between males and during courtship. The fluttering flight associated with courtship in Indigo Buntings is likely homologous with the male flight that precedes copulation in Painted Bunting courtship. The fluttering flight associated with territorial encounters in Indigo Buntings is likely homologous with the Painted Bunting's moth flight. Moth flights performed in similar contexts also occur in fringillids (Condor 1948, Hinde 1955). Wing quivers and moth flights occur in similar contexts and the latter may be a continuation of the wing quiver as the bird changes perches.

The butterfly flight of the Painted Bunting is similar to the undulating flight of the Dark-eyed Junco (*Junco hyemalis*) (Sabine 1952, Balph 1976) and the butterfly flight of the European Goldfinch (*Carduelis carduelis*) (Condor 1948). Communication of the dominance relationship between two birds appears to be the function of the butterfly flight.

The behavior most similar to the feather pull of the Painted Bunting is the pounce of the Song Sparrow (Nice 1943). Pounces in Song Sparrows differ from bunting feather pulls in that pounces also occur during courtship and feathers are not actually pulled. Feather pulls in Painted Buntings were usually directed against females not mated to the attacking males and appear to be a form of defense against trespassing females. Pounces on neighboring females by male Song Sparrows (Nice 1943) and feather pulls by male Painted Buntings never led to solicitations by the females or to copulations.

The courtship displays of Baird's Sparrow (*Ammodramus bairdii*) are similar to the Painted Bunting's, in that the wings are raised and quivered alternately above the back (Bent 1968). Asymetric wing quivering also has been reported in Brown Towhees (*Pipilo fuscus*) (Bent 1968) and Northern Cardinals (*Cardinalis cardinalis*) (Andrew 1961) in unknown contexts and in European Goldfinches in agonistic encounters (Hinde 1955). The general pattern of crouching with raised contour feathers, holding the head level with the body's long axis, and wing quivering occurs in many emberizids (Bent 1968). The differences from the Painted Bunting's courtship pattern that occur in other emberizids include spreading the tail, raising the bill, and vocalizing. Asymetric wing raising is normally absent in the courtship of other emberizids.

The solicitation display of the Painted Bunting is the same as that reported by Andrew (1961) for the emberizines. Female Painted Buntings frequently solicited in the presence of buntings other than their mate and extra-pair copulations occasionally occurred (Lanyon and Thompson, unpubl.).

None of the potential nest-sites examined by Painted Buntings during nest-site exploration was selected as a site for a nest. Many sites are probably examined for each nest that is built, as in the Prairie Warbler (*Dendroica discolor*) (Nolan 1978:102); however, it is possible that the rapid movement and crouching of the female as she is followed by the male play a role in courtship as well as in nest-site selection.

SUMMARY

Descriptions of Painted Bunting (*Passerina ciris*) visual displays and the context in which they occur are based on observations made during four breeding seasons on a barrier island in Georgia. The social context in which the displays occurred was used to infer their function.

Many of these displays are similar to those of closely related species, but the bow display and the form and sequence of courtship displays differ from those of congeners.

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THE BREEDING BIOLOGY OF THE NORTHWESTERN CROW

Robert W. Butler, Nicolaas A. M. Verbeek, and Howard Richardson

In contrast to European *Corvus* species (Coombs 1978), the breeding ecology of the five North American species is poorly known. This is certainly true for the Northwestern Crow (*Corvus caurinus*), which is common on intertidal beaches and the adjacent coastline from Washington to Alaska (A.O.U. 1983). Drent et al. (1964) provided information on laying date, clutch-size, and nesting success of 12 pairs of Northwestern Crows on Mandarte Island, British Columbia. We began our studies of *C. caurinus* in 1973 (Butler 1974, Verbeek and Butler 1981, Verbeek 1982) and present here information about the breeding biology and productivity.

STUDY AREA AND METHODS

The study was conducted from April–August 1976–1983 on Mitlenatch Island (49°57′N, 125°00′W) (Butler 1974) and April–August 1976–1980 on Mandarte Island (48°38′N, 123°17′W) (Tompa 1964), British Columbia. Both islands are inhabited by large numbers of nesting sea-birds (Campbell 1976).

About 60 pairs of crows nested annually on Mitlenatch and from 13–25 pairs on Mandarte. Territories were delineated by marking and connecting the locations of displays and fights between nesting pairs on an aerial photograph (scale 1:5000) or a map (scale 1:1000). Territory size was determined with a planimeter.

Internest distances were measured on the ground with a measuring tape to the nearest 0.5 m or from an aerial photograph. We visited nests every 1–7 days. Nest dimensions were measured before first eggs were laid. The length and width of eggs were measured with Vernier calipers to the 0.05 mm to calculate egg volumes (Hoyt 1979). Eggs and nestlings were weighed with 50-g and 300-g Pesola balances to the nearest 0.5 g. Eggs were numbered with India ink and nestlings were marked with colored Scotch Brand® Plastic Tape on the legs until about 10 days old and then with unique combinations of colored, plastic leg bands. The length of the tarsus was measured by marking the end points on a piece of paper and measuring the distance with a ruler to the nearest 0.5 mm. The incubation attentiveness was obtained by watching individual nests for up to 3 h at various times during the day and recording when the females left the nest and returned to it to resume incubation. The data for brood attentiveness and feeding rates were obtained in the same way.

As only females incubate and brood nestlings, a common corvid habit (Goodwin 1976), we knew the sex of color-banded birds, even if only one member of the pair was banded. Males and females of unbanded pairs were distinguished by size (males are larger) or by various behavioral differences. For instance, males call more frequently, are more aggressive on the territory, and show the "pot-bellied" posture (see Coombs 1978) more intensely than females (pers. obs.). Yearlings were recognized by the brownish cast to the plumage on their

back, wings, and tail (Verbeek and Butler 1981). The data for both islands were pooled when they were not significantly different.

RESULTS AND DISCUSSION

Territory.—Shoreline territories generally included some shrubs or trees, which often held the nest, a section of meadow, and a stretch of beach. Inland territories, not present on Mandarte, differed only in that they lacked a stretch of beach. The mean territory size for both islands combined was 0.49 ± 0.20 ha (N = 61). Compared to other species, Northwestern Crow territories are very small: for instance, 26.7 ± 10.4 ha (N = 41) for the Eurasian Crow (*C. corone*) (Wittenberg 1968), 60 ha for the Black Crow (*C. capensis*) (Skead 1952), and 4 ha for the Little Raven (*C. mellori*) (Rowley 1967). The mean internest distance (17.8 ± 9.6 m, N = 97) between nests of *C. caurinus* in continuous habitat was correspondingly small. The shortest distance between two occupied nests was 4.4 m. Most of the food is obtained off the territory (unpubl.).

Pairs of Northwestern Crows defended nesting territories against all other adults, unrelated yearlings, and some related ones. Of 128 territorial encounters, consisting of displays, chases, and fights, among 14 neighboring pairs without yearling helpers, 104 (81.2%) were performed by males and 24 (28.8%) by females. The role of yearling helpers in territorial defence and reproduction has been discussed elsewhere (Verbeek and Butler 1981).

Nests.—The nest of *C. caurinus* resembles that of the Common Crow, *C. brachyrhynchos* (Bent 1946, Emlen 1942). In 77 nests on Mandarte, cedar (*Thuja plicata*) bark formed part of the nest lining in 72 nests, moss in 45, sheeps wool in 33, grass in 7, and gull feathers in 2. Of 153 nests on Mitlenatch, 152 were also lined with cedar bark and 31 with moss, but 51 held gull (*Larus glaucescens*) feathers, 40 contained grass, 7 held crow feathers, 3 had paper, and 2 contained wool. The use of bark and wool in nests has been reported in other species of *Corvus* as well, for example in *C. corone* (Wittenberg 1968), the Raven (*C. corax*) (Coombs 1978) and the Pied Crow (*C. albus*) (Lamm 1958). Wool occurred in nests on Mandarte because domestic sheep grazed on nearby islands. The high proportion of gull feathers, especially on Mitlenatch, is unusual in the genus *Corvus*. Gull feathers were available on both islands, but perhaps they were used more on Mitlenatch than on Mandarte because of the lack of wool.

Four nests on Mitlenatch were dismantled and weighed. The twigs weighed 52 g in one ground nest and 202 g, 2805 g, and 1007 g in three tree nests. The cedar bark lining from those same nests weighed 236 g,

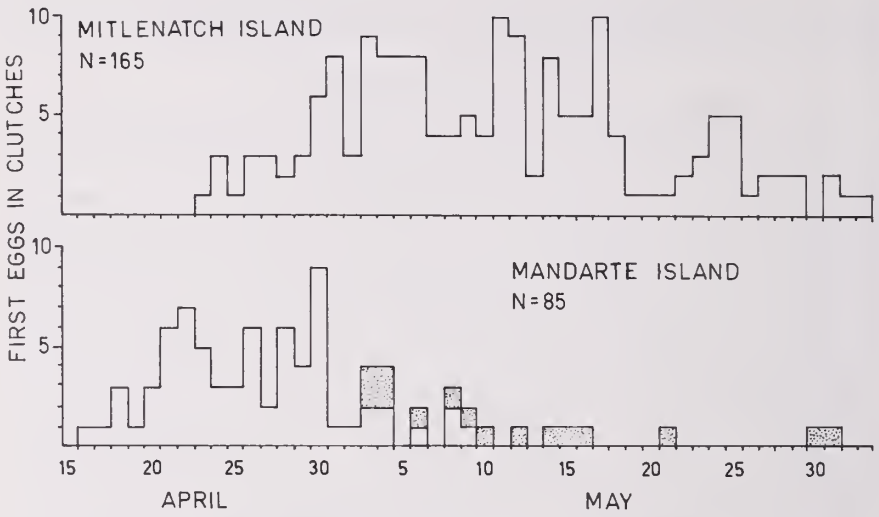

FIG. 1. Clutch initiation dates of Northwestern Crows on Mitlenatch Island and Mandarte Island. Stippled areas represent second nesting attempts. Second nesting attempts on Mitlenatch Island could not be determined with certainty.

15 g, 370 g, and 105 g, respectively, and the moss and grasses combined weighed 170 g, 19 g, 395 g, and 182 g, respectively. Ground nests in general contained fewer twigs and more cedar bark than tree nests. The mean measurements of 23 new tree nests were: 22.1 ± 5.0 cm high, 33.2 ± 4.8 cm in diameter, with a cup depth of 8.9 ± 1.2 cm and a cup diameter of 16.3 ± 1.6 cm.

Nests were built on the ground, in shrubs, and in trees. On Mandarte, 45% of 92 nests were built on the ground compared to 20% of 350 nests on Mitlenatch. The discrepancy between the two islands is in part due to differences in vegetation, Mandarte has few trees and tall shrubs, and in part because some ground nests on Mitlenatch may have been overlooked because of the rugged nature of the island. The percentages of nests built on the ground or in shrubs or trees vary from year to year—the reason for which is as yet unclear. When a sample of 114 nests for which the date on which the first egg was laid was known is divided into 58 early (first eggs laid prior to and including 26 April) and 56 late (after 26 April) nests, then there were significantly ($\chi^2 = 8.90$, df = 1, $P < 0.01$) more ground nests among early than among late nests.

The average height of 51 tree nests on Mandarte was 1.9 ± 0.9 m and for 85 tree nests on Mitlenatch was 2.3 ± 0.9 m. The relatively few nesting

TABLE 1
MEAN VOLUME OF EGGS IN CLUTCHES IN WHICH THE LAYING SEQUENCE OF THE EGGS WAS KNOWN

Position of egg in clutch	Volume (cc) of egg		Significant difference between mean volumes of eggs
	N	$\bar{x} \pm SD$	
1	27	16.6 ± 1.6	1 > 4 ($P = 0.007$), 1 > 5 ($P = 0.03$)
2	24	16.8 ± 1.5	2 > 4 ($P = 0.002$), 2 > 5 ($P = 0.002$)
3	33	16.1 ± 1.3	3 > 4 ($P = 0.03$), 3 > 5 ($P = 0.02$)
4	29	15.5 ± 1.3	
5	8	15.3 ± 0.9	

birds, linear arrangement of territories, and easy visibility on Mandarte provided an opportunity to determine the height of second nests when the first one was predated or disturbed. In all these cases (N = 26), except one, the first and second nest was built on the same territory. The mean height (1.6 ± 0.6 m) of first nests was significantly ($P < 0.05$, Mann-Whitney *U*-test) lower than the mean height (2.7 ± 1.2 m) of second nests.

Northwestern Crows built nests in new sites in most years. On Mandarte, 28.0%, 23.1%, and 26.7% of all nests used in 1978 (N = 25), 1979 (N = 26), and 1980 (N = 30), respectively, were built on top of nests of previous years.

Courtship begging.—The period between the start of courtship begging and egg-laying at five nests was 0, 1, 1, 5, and 7 days. Females begged on or off the territory but once the first egg was laid, courtship begging occurred on the nest or more commonly in its vicinity. Begging continued throughout incubation when the male arrived near the nest to feed his mate.

Eggs and incubation.—First eggs in clutches on Mandarte were laid 6–10 days earlier than on Mitlenatch (Fig. 1). In a sample of 158 eggs for which the laying interval was known, 133 were laid in daily intervals, 24 in 2-day intervals, and 1 in a 3-day interval. We never found 2 new eggs laid within a 24-h period. Laying eggs at daily intervals appears to be general for the genus *Corvus* (Holyoak 1967, Wittenberg 1968). When clutches were abandoned or predated, the first egg in replacement clutches (N = 10) appeared on average 13.6 ± 1.2 days later.

There was no significant difference in the mean egg volumes (Hoyt 1979) among first, second, and third eggs; however, the mean volumes

TABLE 2

MEAN NUMBER OF EGGS THAT HATCHED ON SUCCESSIVE DAYS IN CLUTCHES OF 3, 4, AND 5 EGGS[a]

Day of hatching	3-egg clutches		4-egg clutches		5-egg clutches	
	Eggs hatched		Eggs hatched		Eggs hatched	
	N	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$
First	11	1.82 ± 0.57	23	2.43 ± 0.77	4	2.50 ± 0.50
Second	11	0.91 ± 0.51	23	1.22 ± 0.51	4	1.75 ± 0.43
Third	11	0.27 ± 0.45	23	0.26 ± 0.53	4	0.75 ± 0.43

[a] Nests were visited once per day; only clutches in which all eggs hatched were considered.

of first, second, and third eggs were significantly larger than those of fourth and fifth eggs (Table 1). No comparable data are available for other corvids.

The mean weight of 87 fresh eggs prior to full incubation was 17.8 ± 2.0 g. Emlen (1942) gave an average weight of 16.6 g for 157 fresh eggs of the Common Crow. Eggs lost 18.8% (0.19 g per day) of their initial fresh weight through incubation, and that agrees with 18% loss in weight for a typical bird's egg (Rahn and Ar 1974).

During 147 h of observation at 17 nests only females incubated and they spent an average of 86.0 ± 5.1% of each daylight hour on the nest. The mean inattentive period (N = 65) of females during incubation was 5.6 ± 3.3 min during which they defended the nest, drank, preened, defecated, or were fed. During 151 h of observation, 19 incubating females were fed by their mates an average of 1.4 ± 0.9 times per hour. The mean incubation period (N = 19) from the date of laying of the last egg until that egg and all other eggs in the clutch had hatched was 18.3 ± 0.85 days. One infertile egg was incubated for 33 days and weighed less than 9.0 g when it disappeared, and another infertile egg was incubated for at least 30 days before it was abandoned. Infertile eggs in nests with nestlings disappeared within 8 days.

Northwestern Crows begin to incubate before the clutch is complete, so that the eggs hatch asynchronously (Table 2). In clutches of three eggs, 1.82 ± 0.57 eggs hatched on the same day, the remaining eggs hatched the following day or rarely after 2 days (Table 2). In contrast, in four- and five-egg clutches, incubation did not start until about 2.5 eggs had been laid (Table 2). Lockie (1955) found that Jackdaws (*C. monedula*) began to incubate clutches of four eggs when on the average 2.6 eggs had been laid and Wittenberg (1968) stated that *C. corone* started to incubate when about two eggs had been laid (clutch-size not specified).

TABLE 3
SUMMARY OF NORTHWESTERN CROW BREEDING DATA ON MANDARTE AND MITLENATCH ISLANDS

	Mandarte			Mitlenatch		
	N	N/nest	%	N	N/nest	%
Nests[a]	67			120		
Eggs						
No. eggs	267			479		
No. eggs/nest		4.0			4.0	
No. eggs hatched	208		78	345		72
No. eggs hatched/nest		3.1			2.9	
No. eggs lost	13		5	45		9
No. eggs lost/nest		0.2			0.4	
No. eggs not hatched	46		17	89		19
No. eggs not hatched/nest		0.7			0.7	
Young						
No. young lost	101		49	207		60
No. young lost/nest		1.5			1.7	
No. young fledged	107		51	138		40
No. young fledged/nest		1.6			1.2	
Successful nests[b]	54		81	93		76

[a] Only nests with completed clutches (three or more eggs) in which at least one egg hatched.
[b] Nests from which at least one young fledged.

There was no significant difference in the mean clutch-size and hatching success in the two island populations (Table 3). In a total of 187 nests, there were 44 clutches of three eggs, 101 of four eggs, and 42 of five eggs. The mean clutch-size (N = 187) was 4.0 ± 0.7 eggs. Of a total of 746 eggs, 7.8% were lost to predators, 18.1% failed to hatch, and 74.2% hatched. There are surprisingly few comparative data available for other species of *Corvus*. Wittenberg (1968) found that about 10% of the eggs of *C. corone* failed to hatch.

Nestlings.—Hatching was designated as day 1. At hatching, the nestlings were naked except for tufts of down feathers on the head, dorsal region, wing stubs, and tail and they weighed an average of 14.9 ± 2.1 g (N = 62, Fig. 2). The logistic growth curve

$$\left(W = \frac{A}{1 + e^{-K(t_w - t_0)}}\right)$$

most closely fits the data (Fig. 2). In this equation, W is the weight of the nestling in grams on day t_w, A is the asymptotic weight achieved by the

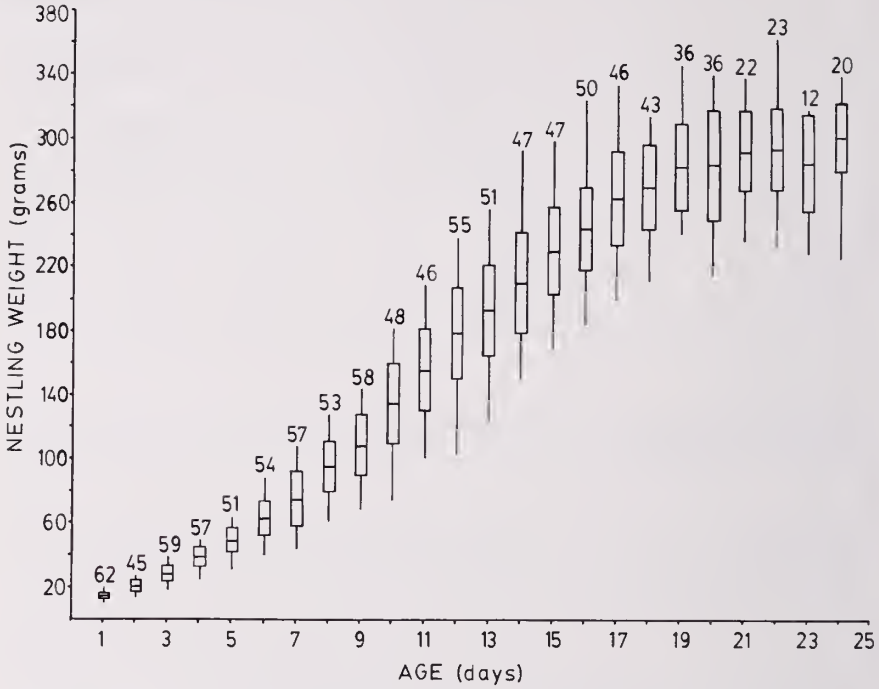

FIG. 2. Change in weight of nestling Northwestern Crows on Mitlenatch Island in 1979 and 1980. Only nestlings that survived to fledging are included. Open bar represents standard deviation around mean, solid line depicts the range and numbers above each point represents the sample size.

average nestling, e is the base of natural logarithms, K is a constant proportional to the specific rate of growth and t_o is the age in days at the point of inflection on the growth curve (Ricklefs 1967). For the Northwestern Crow, A = 305 g, K = 0.298, ½A is 10.8 days, and the time required to grow from 10–90% of A is 14.8 days. The eyes began to open as early as day 5, and they were wide open and a blue iris was apparent at a mean age of 9.0 ± 1.8 days (N = 18), at which time the young weighed an average of 114.7 ± 42.7 g (N = 18). The eyes of nestling Common Crows are slits by day 8 and fully open by day 11 (Emlen 1942). Only females brooded nestlings and they remained very attentive to the nest until the young were about 10 days old (Table 4).

A marked change in behavior occurred when the young were about 12 days old. Prior to that age nestlings begged for food when we jiggled the nest but after that age the same nestlings crouched in the nest and begged reluctantly or not at all. This change in behavior coincided with the timing

TABLE 4
BROOD ATTENTIVENESS OF THREE FEMALE NORTHWESTERN CROWS

Nestling age (days)	Min obs. N	% attentive
1–5	1046	93.1
6–10	138	88.4
11–15	586	30.9
16–18	270	17.8

of the female's increased share in feeding of the young (Table 5) and her reduced nest attentiveness (Table 4). The tips of the folded wing extended beyond the tip of the tail on about day 20 when some nestlings in tree nests began to climb into branches adjacent to the nest. The tarsus attained an adult length of about 50 mm at 16–18 days (Fig. 3) at which time the nestlings began to defecate over the nest rim.

Forty-nine nestlings in 20 nests on Mandarte left the nest permanently at an average age of 32 ± 2.5 days, while 55 nestlings on Mitlenatch did so at an average age of 26 ± 3.4 days. The nestling period on Mandarte agrees well with that of several, slightly larger, other species: 35 days for *C. brachyrhynchos* (Goodwin 1976), 32–33 days for the Rook (*C. frugilegus*) (Goodwin 1976), and 30–36 days (Wittenberg 1968) and 30–34 days (Coombs 1978) for *C. corone*. Premature nest departure on Mitlenatch was presumably due to our presence near nests, whereas on Mandarte the nestlings were observed from a distance.

Fledglings.—Northwestern Crows that fledged from tree nests stayed in trees and shrubs near the nest, whereas fledglings from ground nests moved to nearby trees. Three flightless nestlings from a ground nest moved approximately 30 m through tall grass to reach a nearby tree. Young crows

TABLE 5
FEEDING RATES OF NESTLINGS IN FOUR NESTS BY THEIR PARENTS

Age of nestling	Male		Female	
	No. feedings	Feedings/hour $\bar{x}$ ± SD (%)	No. feedings	Feedings/hour $\bar{x}$ ± SD (%)
1–7 days	44	1.8 ± 0.3 (66.7)	22	0.9 ± 0.4 (33.3)
8–14 days	13	1.1 ± 0.2 (33.3)	26	2.3 ± 0.1 (66.7)
15–21 days	8	0.7 ± 0.2 (32.0)	17	1.6 ± 0.2 (68.0)
22–28 days	6	0.8 ± 0.3 (40.0)	9	1.2 ± 0.2 (60.0)

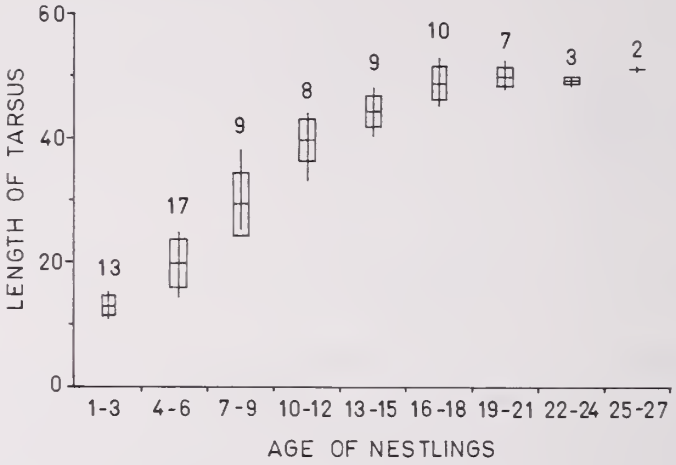

FIG. 3. Change in tarsus length with age of nestling Northwestern Crows on Mitlenatch Island. (Explanation as in Fig. 2.)

clamored toward adults carrying food and eventually began to follow closer to the food source 2–3 weeks following nest departure. Once the young could fly the offspring of two or more families mixed together.

Fledging success, defined as the number of eggs hatched that fledged young, was low on both islands (Table 3). Significantly ($P < 0.05$) more young fledged on Mandarte than on Mitlenatch but the percentage of nests that fledged at least one young was about the same (Table 3). Among 47 nestlings that disappeared at a known age, 27 (57%) were lost within the first 7 days following hatching, 13 (28%) between 8 and 14 days, and 7 (15%) between 15 and 20 days. None disappeared after 21 days. Similar results have been reported for *C. corone* (Tenovuo 1963) and *C. monedula* (Zimmermann 1951).

Mortality among fledgling Northwestern Crows based upon sightings of colorbanded young on Mitlenatch was low in the 9 weeks following fledging. Thirty-eight (75%) of 51 fledglings seen in the first week following fledgings were still alive 9 weeks later. All 38 juveniles were seen at least once during each of the 9 weeks. Among 12 fledglings from early nests (fledged on or before 15 June), 11 were seen between 22 July and 26 August (median date 22 August), while among 14 late nests (fledged after 15 June), only seven birds were seen between 1 July and 26 August (median date 13 July). Mitlenatch is separated from the nearest land by an often windy 5 km of water and it is very unlikely that fledglings attempted to leave the island during those first 9 weeks. Attacks by Glau-

cous-winged Gulls (*Larus glaucescens*) were a major source of mortality on both islands when the fledgling crows landed on gull territories.

Ten fledglings on Mitlenatch were observed almost daily following departure from the territory. They were first seen to feed themselves at an average of 27.6 ± 7.4 days after fledging. On Mandarte one fledgling was fed sporadically 77 days after fledging.

SUMMARY

Northwestern Crows (*Corvus caurinus*) were studied during April–August 1976–1983 on Mitlenatch and Mandarte islands in Georgia Strait, British Columbia. Nesting territories ($\bar{x}$ = 0.49 ha) and internest distances ($\bar{x}$ = 17.8 m) were small compared to other species of *Corvus*. Nests were built on the ground or in shrubs and trees. Nests built early in the season tended to be ground nests as compared to those built later. The average height of tree nests was 2 m. About 25% of the nests each year were built on top of nests of previous years. Most eggs were laid at daily intervals. The mean weight of fresh eggs was 17.8 g and eggs lost 18.8% of their initial weight during the incubation period ($\bar{x}$ = 18.3 days). Fourth and fifth eggs were significantly smaller than first, second, and third eggs. Incubation began when an average of 2.3 eggs had been laid in a clutch. The mean clutch-size was four eggs. Hatching success was 74%. Nestlings weighed 14.9 g at hatching and 300 g about 4 weeks later. About 79% of the nests fledged one or more young.

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MOVEMENT AND MORTALITY ESTIMATES OF CLIFF SWALLOWS IN TEXAS

PATRICIA J. SIKES AND KEITH A. ARNOLD

The Cliff Swallow (*Hirundo pyrrhonota*) has been studied extensively in various parts of the country (Buss 1942, Emlen 1954, Myres 1957, Mayhew 1958, Samuel 1971, Grant and Quay 1977, Newnam 1980). Most of these studies deal with growth rates of young, basic biology, and behavior. Only Mayhew (1958) undertook a long term banding project to determine movements and mortality of Cliff Swallows. Samuel (1971) developed life history equations for Barn (*H. rustica*) and Cliff swallows, but based his results on models rather than years of data collection. In this paper we present data which document Cliff Swallow movements through successive years and give estimates of mortality for both adult and juvenile swallows.

METHODS

A trapping and banding operation begun by Newnam (1980) in 1974, has been continued by us through 1983. In our area, Cliff Swallows nest in cement drainage culverts under roads. Adults were captured by closing both ends of the culverts with 6 mm mesh minnow seines, approximately 0.5 h before dawn (Mayhew 1958). Headlamps were used to flush birds from nests. The swallows could then be captured by hand as they clung to the net, and placed in collapsible fish baskets used as holding cages. In 1981 through 1983, adults also were captured while on their nests. We quietly entered the culverts before dawn, without lights, and plugged the openings of the nests with cotton. At daybreak we re-entered the culvert and removed the cotton and the adults. We successfully trapped pairs on the nest only while they were sitting on eggs. Once the eggs hatched, either one or no parent was present. The adults were measured (wing chord, tarsus length, and weight), banded with U.S. Fish and Wildlife Service bands and released.

Young birds were banded when approximately 2 weeks old. They were removed by carefully breaking away the outside and top edges of the nest, enough to get two or three fingers in to remove the young. No measurements were taken on the young except during Newnam's (1980) growth rate study.

Birds were banded in six major colonies near Somerville, Texas: four in Burleson Co. and two in neighboring Washington Co. (Fig. 1). Usually only one colony of approximately 100–150 nests was active each year. An unusually high number of colonies were active in 1975 and 1983 and swallows at all five colonies active in these years were subjected to trapping at least once. Adults were captured in the only two active colonies in both 1981 and 1982.

Mortality estimates were derived using survival tables (Downing 1980). The two estimates acquired were tested in a simulated computer run to determine which estimate best fit our long-term recapture data.

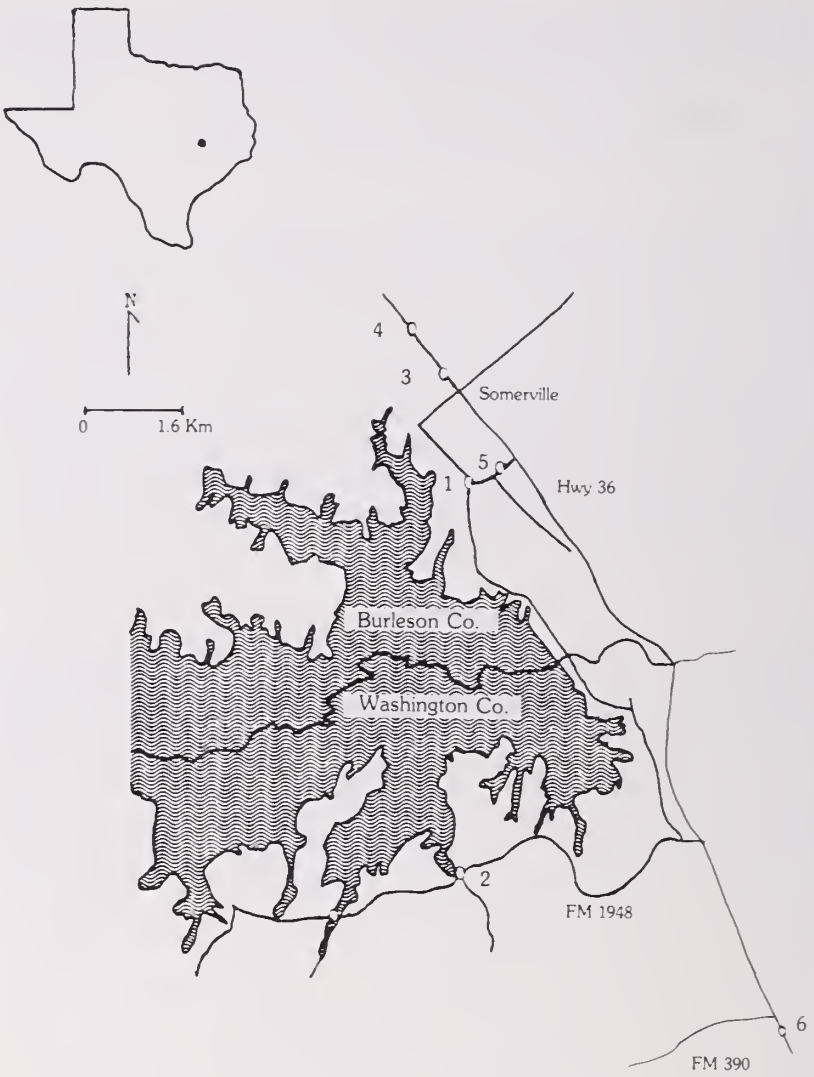

FIG. 1. Locations of colonies in Burleson and Washington counties, Texas.

RESULTS AND DISCUSSION

Movement.—Mayhew (1958), Samuel (1971), and Newnam (1980) have documented year-to-year movement of Cliff Swallows. For our study, Table 1 shows the percentage of adult and young Cliff Swallows returning to their banding culvert in subsequent years. Analysis of the first year's

TABLE 1

PERCENTAGES OF CLIFF SWALLOWS RETURNING TO THEIR BANDING CULVERT IN THE YEARS FOLLOWING BANDING

Year	% adults	% young
1st	45 (150/336)[a]	48 (136/285)
2nd	13 (17/132)	10 (13/132)
3rd	10 (5/50)	5 (2/38)
4th	34 (12/35)	55 (11/20)

[a] Numerator represents actual number of swallows recaptured in banding culvert, denominator represents total number of swallows recaptured in that age class.

returns reveals that only 45% (150) of the 336 recaptured adults and 48% (136) of the 285 recaptured juveniles nested in the same culvert as the previous year. In subsequent years, both adults and young tended to nest in other culverts. Possibly, this is a result of an increase of swallow bugs (*Oeciacus vicarius*) in the culverts. As suggested by Chapman (1973), the birds seem to change culverts to avoid these ectoparasites.

The movement of both adults and young to other culverts in the years after banding does not seem to follow Mayhew's (1958) loyalty hypothesis, which states that once a swallow nests in a particular culvert it has a strong desire to return to that culvert. However, four of the six culverts in our study area are within 2.0 aerial km of each other and thus lie within the same 10 min lat.-long. block. Only one of these culverts was active in each year of the study, except 1975 and 1983 when two were active, but the second culvert had fewer than 100 birds in each year and these birds mostly comprised renesters. In any one year, the majority of the population was concentrated in one of the four culverts. We have shown that individual birds will use different culverts in successive years and

TABLE 2

PERCENTAGES OF CLIFF SWALLOWS RETURNING TO CULVERTS IN THE SAME 10 MIN LAT.-LONG. BLOCK AS THEIR BANDING CULVERT IN THE YEARS FOLLOWING BANDING

Year	% adults	% young
1st	79 (267/336)[a]	74 (211/285)
2nd	80 (106/132)	58 (77/132)
3rd	76 (38/50)	37 (14/38)
4th	76 (26/35)	60 (12/20)

[a] Numerator represents actual number of swallows recaptured in same block, denominator represents total number of swallows recaptured for that age class.

TABLE 3
NUMBER OF ADULT CLIFF SWALLOWS CAPTURED OR KNOWN TO BE ALIVE

Age (years)	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
0–1[a]	13	363	100	120	134	146	119	176	393	528
1–2		3	125	10	36	33	30	21	58	109
2–3			3	73	5	18	21	17	18	22
3–4				2	31	1	9	14	14	8
4–5					2	22	1	6	14	4
5–6						—	11	—	5	10
6–7							—	3	—	3
7–8								—	3	—
8–9									—	2

[a] Represents number of unbanded adults captured, banded, and released each year.

thus we consider these four culverts to be used by one breeding population. Table 2 shows the change in percentages of returning birds if the four culverts are treated as the same "colony." The adults and juveniles seem to remain loyal to their breeding "colony" even though the actual culvert may be different. Approximately 79% (267) of the 336 recaptured adults and 74% (211) of the 285 recaptured juveniles return to the same "colony" to breed in the first year after banding. The percentage of returns remains high in subsequent years. No differences were found between the rate of return of each sex. Apparently, dispersal is not linked to sex or age.

Mortality.—Few estimates of the mortalityof Cliff Swallows exist. Mayhew (1958) estimated a 50% annual adult mortality, based on recaptures. Samuel (1971) estimated a 65% annual mortality for young swallows over their first winter. He arrived at this percentage through estimated life equations. Harwood and Harrison (1977) estimated a 60% adult and 80% juvenile mortality of Sand Martins (=Bank Swallow [*Riparia riparia*]) based on recovery data. Mead (1979) estimated 65% adult and 77% juvenile mortality of Sand Martins based on recoveries. As Cliff Swallow recovery data are scarce, our data are based on recaptures.

Tables 3 and 4 show the number of adults and juveniles, respectively, that were captured or known to be alive from subsequent recaptures for each year. Age 0–1 represents the number of unbanded adults and nestlings, respectively, that were captured, banded, and released each year. We used these data to calculate calculate survival tables (Downing 1980). Table 5 shows the survival rates based on a composite of all adult and all juvenile cohorts. Survival rates averaged 0.460 for adults and 0.537 for juveniles. Another method used was to determine the overall mean

TABLE 4
NUMBER OF JUVENILE CLIFF SWALLOWS CAPTURED OR KNOWN TO BE ALIVE

Age (years)	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
0–1[a]	315	455	0	0	75	74	175	670	706	755
1–2		37	67	—	—	7	4	26	104	137
2–3			36	58	—	—	4	3	21	39
3–4				26	19	—	—	4	2	9
4–5					16	16	—	—	3	1
5–6						12	10	—	—	1
6–7							8	6	—	—
7–8								6	5	—
8–9									5	—
9–10										4

[a] Represents number of nestlings banded and released each year.

of each cohort's annual survival rate. For example, 363 unbanded adults were captured in 1975 (Table 3). Of these, 125 were recaptured or known to be alive in 1976, 73 in 1977, etc. The calculated survival rate was 125/363 or 0.344 and 73/125 or 0.584, etc. This calculation was done for each cohort through each year. These individual survival rates were summed and then divided by the total number of calculations or the total number of yearly intervals for each cohort. The adult mean survival rate was 2020.8/37 = 0.546. The juvenile mean survival rate (Table 4) was 1729.4/31 = 0.558.

To determine which of the two calculations of adult survival (0.460 vs 0.546) was more realistic, we tested each in a simulated computer run against our data. The computer run allowed us to compare the theoretical number of adults that should survive to any given year based on each mortality estimate, against the actual number we recaptured. From these tests we found that the 0.546 survival rate best fit our long-term recapture data. Overall, a 45% mortality of both adults and juveniles appears to represent mortality for our populations.

The problem with determining a differential mortality for adults and juveniles must be resolved in the first year after banding. Table 5 shows a tremendous decrease in the survival of both adults and juveniles the first year after banding. Twenty-seven percent (425) of the 1564 adults banded through 1982 are recaptured at some time, whereas, only 16% (382) of the 2470 juveniles banded through 1982 are ever recaptured. So 11% more adults survived than juveniles through their first year suggesting a higher first year juvenile mortality. However, of those swallows that are

TABLE 5

SURVIVAL TABLE BASED ON A COMPOSITE OF ALL ADULT COHORTS AND ALL JUVENILE COHORTS

Age (years)	Adults		Juveniles	
	Pop. size[a]	Survival rate[b]	Pop. size[a]	Survival rate[b]
0–1	1564	0.272	2470	0.155
1–2	425	0.416	382	0.421
2–3	177	0.446	161	0.373
3–4	79	0.620	60	0.600
4–5	49	0.531	36	0.639
5–6	26	0.231	23	0.609
6–7	6	0.500	14	0.786
7–8	3	0.667	11	0.455
8–9	2	1.000	5	0.800
9–10	—	—	4	1.000

[a] Summation of all numbers in each age class from Tables 3 and 4, respectively, excluding age 0–1 in 1983 since no recaptures have been made from that year.

[b] Population size of second age class population size of first age class, i.e., 425 1564 = 0.272.

subsequently recaptured the mortality decreases to approximately 35% for adults and juveniles alike. This suggests a high mortality or dispersal after the initial banding, but once they are recaptured they are likely to be recaptured again in successive years.

We attempted to use Jolly's (1965) method to estimate survivorship based on recapture data. Lack of consistency in our banding effort resulted in low numbers of recaptures in some years which caused the calculated estimates to be untenable. Many of our recaptures were not caught each year and were seen only once or twice in the 9 years of study. Four of our six 9-year-old birds were recaptured for the first time in 1982 or 1983. Nine years is the longevity record for Cliff Swallows (M. K. Klimkiewicz, pers. comm.). This gap in recapture time caused problems when we attempted to use the Jolly method.

In general, our mortality estimates did not vary greatly from Mayhew's (1958). An average of 45% annual mortality for adult and juvenile Cliff Swallows was estimated from our data as opposed to 50% for Mayhew. Samuel's (1971) estimate of 65% first year juvenile mortality was lower than our estimated 84% mortality. However, we also had a high first year adult adult mortality of 73%. These high percentages could represent dispersal, as well as mortality. Cliff Swallows are spreading rapidly southward in Texas and many of these "missing" birds could be pioneering new colonies.

SUMMARY

We used 9 years of banding data to study movement patterns and to estimate mortality of Cliff Swallows (*Hirundo pyrrhonota*). Adult swallows averaged a 79% return rate to their breeding "colony," but not necessarily to their breeding culvert. Young swallows averaged a 74% return rate to their breeding "colony." No significant difference was found between the rate of return of either sex. Using Downing's (1980) survival tables, we calculated a 45% annual mortality for both adults and juveniles. Juvenile first year mortality was 11% higher than adult mortality. Six 9-year-old swallows were captured during the study, tying the existing longevity record.

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EFFECT OF EDGE ON BREEDING FOREST BIRD SPECIES

Roger L. Kroodsma

The clearing of forests often creates forest edges where an edge effect reportedly causes increased densities and diversities of birds and other wildlife (Lay 1938, Johnston 1947, Anderson et al. 1977, McElveen 1979, Strelke and Dickson 1980). The clearing also causes loss of forest habitat and often results in forest fragmentation. In addition to the effects of habitat loss, forest fragmentation may be responsible for an observed decline in abundance of certain bird species in the remaining forest fragments (Robbins 1979, Whitcomb et al. 1981). The decline of birds in the forest fragments theoretically could result from the small size and isolation of the forest islands (MacArthur and Wilson 1967), increased predation on nestlings near edges (Gates and Gysel 1978), negative responses of forest interior birds to edges (Kroodsma 1982a), brood parasitism by cowbirds (*Molothrus* sp.) near edges (Brittingham and Temple 1983) or from disturbances other than forest clearing itself (e.g., human activity, industrial facilities) (Robbins 1979).

The present paper examines the effects of power-line corridor edges on the density of individual breeding bird species of forests, including several of the species that have apparently declined in forest fragments (Whitcomb et al. 1981). The study is based on a total of four territory-mapping censuses, each in a different year, on two large forest plots adjacent to power-line corridors. An earlier paper (Kroodsma 1982a) examined edge effect on forest birds at the community level rather than at the species level and covered only 2 years of censusing on one plot. The purpose of the current paper is twofold: (1) to determine the sensitivity of individual bird species to edges and to forest fragmentation; and (2) to study edge effect based on territory mapping from edges to deeper forest. Previous studies of birds along edges did not examine the density of territories from the edges to deep habitat interior. Most studies were either based on frequencies of observations or registrations rather than on territories (Lay 1938, Anderson et al. 1977, Strelke and Dickson 1980) or involved little or no forest interior (Johnston 1947, McElveen 1979). The results of this study will be useful in assessing the effects on various forest bird species of creating power-line corridors and other clearings (e.g., wildlife clearings) in forests.

STUDY AREAS

Two hardwood forest plots were selected at the Department of Energy's Oak Ridge Reservation in eastern Tennessee. The Reservation occupies about 15,000 ha in the Ridge and Valley Province. About 72% (10,800 ha) is forested, 13% (1950 ha) is pasture, and about 15% (2250 ha) consists of three industrial complexes. The forested areas consist of 37% hardwoods, 20% hardwood-pine (*Pinus* spp.), 17% planted pine, 16% natural pine, and 10% various mixtures of cedar (*Juniperus* sp.) with hardwood and pine. Areas surrounding the Reservation contain proportionately more cleared lands in pasture and crops.

One study plot was located on the Reservation and the other was on Haw Ridge adjacent to the eastern end of the Reservation. Both plots consisted primarily of oak (*Quercus* spp.)-hickory (*Carya* spp.) forest and were rectangular, with one of the longer sides being the forest edge along a power-line corridor (Fig. 1). The remaining plot edges were bounded by additional extensive hardwood or hardwood-pine forest. The major topographic features (ridges and a stream valley) and vegetational features of the plots were perpendicular to the power-line corridors rather than parallel. Thus, any effect of the corridor edge on birds should not be confounded by ecological gradients (e.g., a gradient from ridge top to stream) associated with these other environmental features. Prior to about 1935, the forests were probably dominated by American chestnut (*Castanea dentata*), which is now absent from the plots as a mature tree due to the chestnut blight. Elevations on the plots range from 245–350 m above mean sea level. Both power-line corridors were initially cleared in 1964 and 1965 and are oriented roughly north and south. The Reservation corridor was widened in 1969. Both corridors are maintained by mechanical cutting with a large rotary blade on a tractor usually once every 4 years. Cutting is conducted up to the forest edges, which are thus very narrow and distinct.

The Reservation plot covered 21.4 ha and was censused in 1977 and 1979. It extended 800 m along a 79-m-wide corridor and 268 m from the corridor edge into the forest. Aerial photographs taken in 1935 showed that at that time about an eighth of the plot was a cleared pasture and the remainder consisted of forest with a highly broken canopy, which possibly resulted from selective logging and a die-off of American chestnut. A small permanent stream with a gradual gradient of 2% runs through the south half of the plot, perpendicular to the corridor. A long narrow pine plantation, 55 m wide, is located about 40 m from and parallel to the stream. The north half of the plot is on a low ridge with gentle slopes and has two small stands of immature forest totaling about 2 ha adjoining the corridor. The remainder of the plot is medium-aged forest.

The Haw Ridge plot was censused in 1980 and 1981. The plot extends 948 m along a 107-m-wide corridor. In 1980 the plot extended 213 m into the forest and covered 20.2 ha. In 1981 it was enlarged to extend 488 m into the forest and covered 46.3 ha. On 1935 aerial photos, the entire plot consisted of medium- to old-aged hardwood forest with a slightly broken canopy. The northern half of the plot is on a highly dissected ridge with steep slopes. The southern half is an upland area at a lower elevation than the ridge and has a few small intermittent streams and primarily gentle slopes.

METHODS

Census procedure.—Breeding birds were censused by the territory mapping technique (IBCC 1970, Robbins 1978, Svensson 1978). To provide for systematic coverage, I divided the Reservation plot lengthwise into two halves, with one half adjacent to the corridor and the other half in deeper forest. Down the middle of each half and parallel to the corridor edge, I marked a line with grid points 30 m apart. I mapped bird locations as I moved

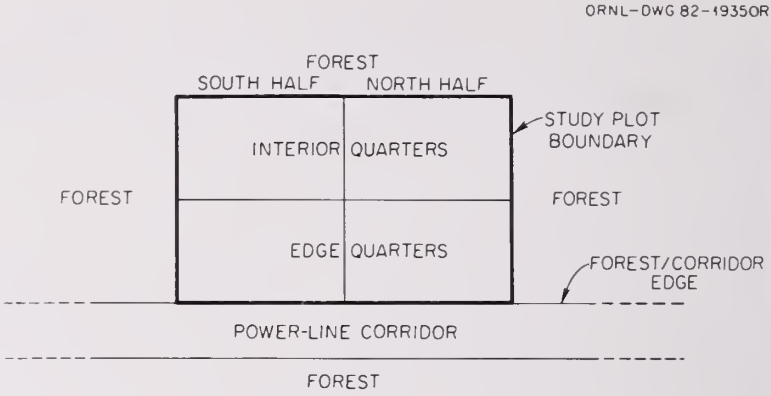

FIG. 1. Layout of the two forested study plots and power-line corridors (not to scale).

slowly down the lines and stood for an equal time at each grid point. Singing or calling males within each entire half of the plot (i.e., within 67 m of each grid line) could be easily heard from the grid points. Further details on censusing procedure in this plot are given elsewhere (Kroodsma 1982a). On Haw Ridge I established eight grid lines that were 122 m apart and perpendicular to the power-line corridor. Grid points on the lines were 30 m apart in 1980, but 61 m apart in the larger 1981 plot. The outermost grid points were 30 m outside the plot. Equal time was spent at each point. No part of the plot was more than 61 m from the grid lines.

The Reservation plot was visited 13 times in 1977 and 12 times in 1979. The Haw Ridge plot was visited 13 times in 1980 and 11 times in 1981. The large size of the Haw Ridge plot in 1981 required two mornings for a complete visit. Visits were conducted between 05:45 and 09:30 EDT, 10 May–15 June. They began at different places on the plots to avoid time-of-day bias and were not conducted during rainy or windy conditions. The vast majority of registrations were songs and calls rather than sightings. The occurrence of contemporary registrations of singing males played a major role in my identification of separate territories. The degree to which forest bird territories extended into the power-line corridors was determined by territory mapping on the Haw Ridge corridor in 1980 and 1981, on the Reservation corridor in 1976 and 1980, and on several other corridors in a previous study (Kroodsma 1982b).

Bird registrations recorded on the visit maps during censusing were later transferred to species maps (one map for each species in each year). Territorial boundaries were drawn with curved lines (convex and concave) that closely fit the clusters of registrations. Lone registrations that appeared to be outliers of a territory were connected to the main body of the territory by drawing narrow territorial extensions. Thus, the contribution of outlier registrations to territory size was minimized so that any estimated territory tended to be a used territory rather than a maximum territory as defined by Odum and Kuenzler (1955). Because the location and configuration of each territory with respect to the edge were of primary interest in this study rather than territory size, it was not important to use one of the standard methods (e.g., the minimum convex polygon method, Ford and Myers 1981) of delineating territories for the purpose of estimating territory size. However, it was important not to include large intraterritorial spaces without registrations in order to avoid inaccurate estimates of territory location and configuration. Densities were calculated as the

number of males per 40 ha, including only the estimated fractions of territories within the study plots.

Data analysis.—The potential effects of the forest edges on birds were examined by plotting bird density vs distance from the edge and testing statistically for significant trends. To calculate density at various distances from the edge, I divided the species maps lengthwise into strip transects representing approximately 11-m-wide strips through the forest plots (the width differed slightly between plots). Thus, a 264-m-wide plot would have 24 strip transects. The first strip transect for each plot was adjacent to the power-line corridor, and the remaining transects were successively deeper into the forest. The fraction of each territory in each transect was determined. Population density in each transect was calculated by summing the territorial fractions located within the transect and converting to numbers of territories per 40 ha, and plotted on distance from the edge. Thus, each transect yielded one coordinate (data point) for each species in each year that the species was present. Forest bird territories rarely extended into the corridor. Therefore, in calculating density I assumed that all forest bird territories near the corridor edge lay completely within the plot.

Although the territory mapping method is traditionally used for estimation of bird density on entire plots rather than on narrow transects as in this study, I feel that my more specialized application of the method is valid. Because I mapped territories on large plots and only subdivided the plot maps into narrow transects after censusing and delineation of territories were completed, boundary effects experienced in sampling small plots (Marchant 1981, Verner 1981) were not a factor in this more specialized approach. I should also point out that each density estimate for a transect is by itself of no significance in this paper and is not meant to indicate the bird density at a particular distance from the forest edge. Rather, the density estimates are used only to identify trends in density from the edge to forest interior.

Differences in bird density between near-edge and deep-forest areas were tested statistically in two steps. First I used linear regression to test for trends in each species' density from the corridor edge to 268 m into the forest. The density data for each species were pooled over the 4 years during which censusing was conducted. Differences between years and between plots were not tested because of inadequate sample sizes (i.e., the numbers of territories) in each year or each plot. Regression analysis was performed on the pooled data. Species not showing significant trends in pooled density from the edge to deep forest were deleted from further testing, because, if the pooled sample size were sufficient and real trends did exist, the trends should have shown up at this stage of testing.

This regression analysis could not be used to determine which species actually responded to edge, because the density values for the strip transects were not independent; i.e., a high density in one strip transect was likely to be associated with a high density in adjacent strip transects, because each territory covered portions of many strip transects. For example, all 24 strip transects in the Reservation plot were intersected by three territories of Red-bellied Woodpeckers in 1979 (see tables for scientific names). Although the resulting 24 density values showed a significant trend, a sample size of only three territories does not justify inferring that there is a response at the species level.

Therefore, data for each species whose density showed a statistically significant regression were then analyzed by individual year to determine whether the trend was consistent among years and plots. Each plot was divided into equal rectangular quarters, two quarters adjacent to the power-line corridor (edge quarters) and two in deeper forest (interior quarters) (excluding the portion of the Haw Ridge plot from 268–488 m into the forest in 1981) (Fig. 1). Density was calculated for each quarter in each year. The density estimates for an interior quarter and the estimate for the adjacent edge quarter formed one pair of observations. A total of eight pairs of observations (N = 16) were available for each species that occurred

in each pair of edge and interior quarters in each of the 4 years. The differences in density between edge and interior quarters were tested by analysis of variance with paired comparisons after transforming the data to natural logarithms, and by the Wilcoxon signed-ranks test, a nonparametric method (Sokal and Rohlf 1969:328, 399). The log transformation improves the normality of the data, independence of the variance and the mean, and the additivity of the effects (Snedecor and Cochran 1967:325–330). For the Acadian Flycatcher, whose territories were relatively small, each plot was divided into six rectangles instead of four, and the mean density value for each pair of interior rectangles was used in the statistical comparison with the respective edge rectangle.

For both analysis of variance and the signed-ranks test, the pairs of observations must be independent. I feel that this requirement was adequately satisfied because: (1) the habitats of the north and south halves of each plot were different, and (2) the plot quarters were relatively large. Thus, I believe that, apart from any effect of the forest edge, the locations of territories within one half of each plot had inconsequential effect on, or correlation with, the locations of territories in the other half. Both tests have the paired comparisons design. This design was more efficient than completely randomized analysis of variance because of the often large differences in density between north and south halves of the plots.

RESULTS

The plots of population density on distance from the power-line corridor are presented in Fig. 2. Several of the species plots are characterized by more or less regularly spaced peaks and lows of density (e.g., Acadian Flycatcher, Scarlet Tanager, Blue-gray Gnatcatcher, Blue Jay). The peaks may represent the location of the core areas of territories, and the lows may represent the buffer areas between territories. A core area is a central location in the territory where most singing occurs and where the birds are observed most often, and a buffer zone is the space between song territories where virtually no singing occurs (Stenger and Falls 1959, Zach and Falls 1979). The fact that the plots are characterized by distinct peaks rather than by straight or irregularly fluctuating lines indicates that territories tended to line up in rows parallel to the edge of the corridor (Kroodsma 1982a). One row of territories adjacent to but not extending into the corridor formed the first peak, and a second row of territories deeper into the forest formed the second peak. This result would be expected if birds tended to use all available space in the forest and if the corridor edge neither attracted nor repelled the birds. The territories of forest birds other than the cardinal and towhee, both edge species, did not extend into the corridor. These results suggest that the corridor/forest edge forms a natural border that affects the location of territories, both near the edge and deeper into the forest.

Several of the same species that showed density peaks had low densities at the edge of the corridor. This may have resulted from the tendencies of the territories delineated on species maps to be more circular than rectangular and to average less territorial area per registration at the pe-

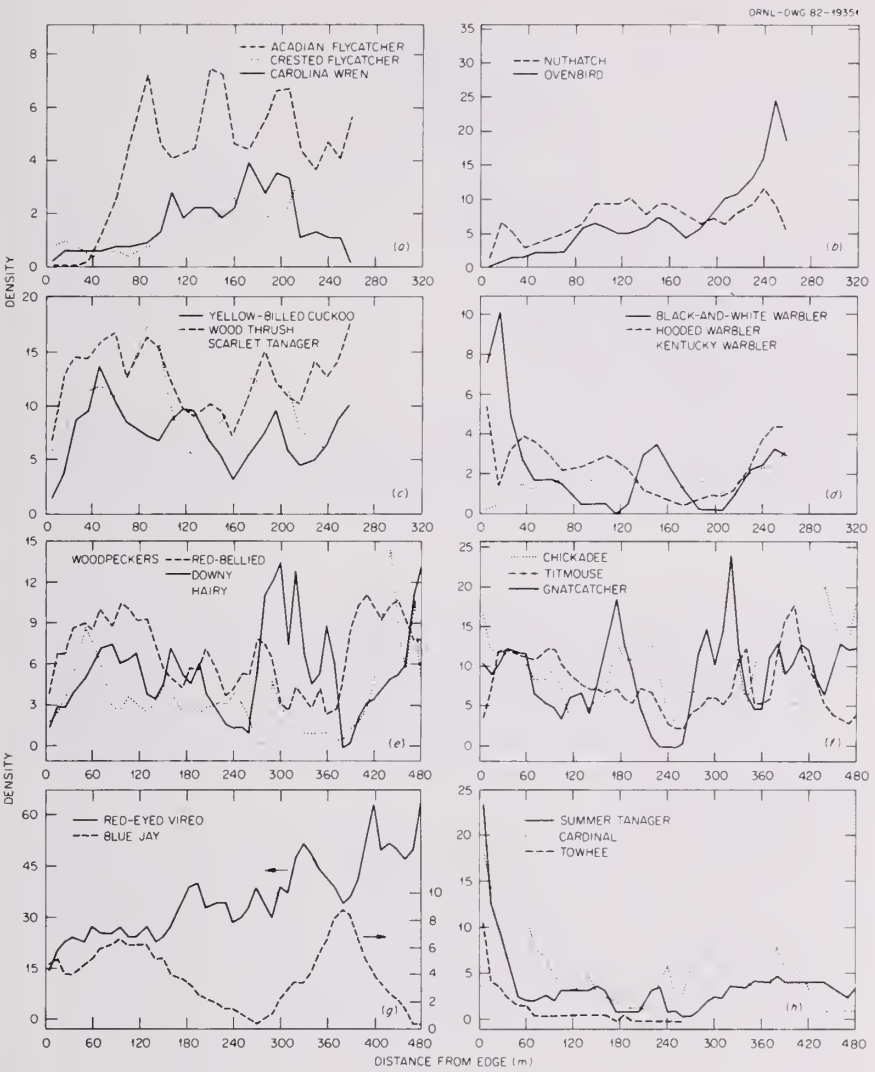

FIG. 2. Plots of bird density (pairs/40 ha) from the corridor/forest edge into deeper forest.

riphery than in the center of the territory (Kroodsma 1982a). Thus, on a per unit area basis, smaller fractions of forest bird territories would be expected to lie along a natural border (i.e., the forest-corridor edge) than slightly removed from the border (i.e., closer to the territorial core area).

TABLE 1

SPECIES NOT INDICATING ANY POTENTIAL EDGE EFFECT AND THEIR SAMPLE SIZES OVER BOTH PLOTS AND ALL YEARS

	Sample size (N)[a]		
	0–268 m (N_1)	268–488 m (N_2)	Total N
Yellow-billed Cuckoo (*Coccyzus americanus*)	21	4	23
Hairy Woodpecker (*Picoides villosus*)	11	3	13
Downy Woodpecker (*P. pubescens*)	13	4	16
Carolina Chickadee (*Parus carolinensis*)	22	8	29
Wood Thrush (*Hylocichla mustelina*)	35	5	37
Hooded Warbler (*Wilsonia citrina*)	7	0	7
Scarlet Tanager (*Piranga olivacea*)	29	6	32
Blue-gray Gnatcatcher (*Polioptila caerulea*)	18	6	24

[a] N is the number of territories measured, some of which were not located completely within the plots. Because some territories extended into both distance categories of the Haw Ridge plot and were counted in the sample size of both categories, the total N frequently is less than the sum of N_1 and N_2. N_1 represents 4 years of censusing whereas N_2 represents only 1 year.

Correspondingly, the density estimates, which were based on fractions of territories in narrow strip transects, would be less along the edge.

In several species (Blue Jay, chickadee, titmouse, Wood Thrush, gnatcatcher, Black-and-white Warbler), the core areas of territories adjacent to the corridor appeared to be shifted toward the edge. However, the density of territories was not significantly greater ($P > 0.10$) near the edge than in deeper forest.

Regression analyses based on data pooled over plots and years indicated that densities of about a third of the bird species did not depend on distance from the edge. These species are listed in Table 1. Pooled densities of each of the 14 remaining species (Table 2) showed significant ($P < 0.05$) trends from the corridor edge to deeper forest. These species were therefore further tested for year-to-year consistency.

Both the analysis of variance and the signed-ranks tests indicated that densities of 5 of the 14 bird species analyzed were significantly associated ($P < 0.05$) with distance from the corridor edge (Table 2). Species that were denser near the edge than in deeper forest were the cardinal ($P < 0.01$), Rufous-sided Towhee ($P < 0.05$), and Summer Tanager ($P < 0.05$) (Table 2). The Ovenbird ($P < 0.01$) and Acadian Flycatcher ($P < 0.05$) were denser in the forest interior.

The Blue Jay and Tufted Titmouse also indicated significant edge effects within the distance from the corridor edge to 268 m into the forest, which was the distance over which all species were analyzed. However, beyond

TABLE 2
STATISTICS FOR SPECIES INDICATING A POTENTIAL EDGE EFFECT

	Sample size (N)[a]			Probability level[b]	
	0–268 m (N_1)	268–488 m (N_2)	Total N	Analysis of variance	Signed-ranks test
Red-bellied Woodpecker (*Melanerpes carolinus*)	18	8	23	>0.05	NS
Crested Flycatcher (*Myiarchus crinitus*)	4	0	4	—[c]	—
Acadian Flycatcher (*Empidonax virescens*)	11	3	14	*	*
Blue Jay (*Cyanocitta cristata*)	10	2	12	*	*
Tufted Titmouse (*Parus bicolor*)	22	6	26	**	*
White-breasted Nuthatch (*Sitta carolinensis*)	18	7	22	>0.25	NS
Carolina Wren (*Thryothorus ludovicianus*)	6	0	6	—[c]	—
Red-eyed Vireo (*Vireo olivaceous*)	68	31	93	>0.10	NS
Black-and-white Warbler (*Mniotilta varia*)	4	2	5	—[c]	—
Ovenbird (*Sieurus aurocapillus*)	21	5	23	**	**
Kentucky Warbler (*Oporornis formosus*)	6	1	6	>0.25	NS
Summer Tanager (*Piranga rubra*)	11	2	13	**	*
Cardinal (*Cardinalis cardinalis*)	19	4	21	**	**
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	8	0	8	*	*

[a] Same as in Table 1.
[b] The probability level represents all 4 years of censusing; * $P < 0.05$, ** $P < 0.01$, NS = not significant.
[c] No significance level was estimated for species absent in one or more years.

268 m their densities increased to levels about equal to densities in the forest nearer the corridor (Fig. 2), and a regression of their densities from the edge to 488 m was not significant ($P = 0.09$ and 0.22, respectively). Therefore, there probably was not a significant edge effect. These two species had larger estimated territories than the other species. Therefore, analysis of their trends over the 488-m distance rather than the 268-m distance was probably more realistic. The significant results over the 268-

m distance may have resulted from shifts of the core areas of the near-edge territories toward the edge.

The Crested Flycatcher, Carolina Wren, Black-and-white Warbler, and Hooded Warbler were present in only 2 or 3 years and were not analyzed. In addition, many other species occurring less frequently in the forest plots (Kroodsma 1984) were not analyzed because of an insufficient quantity of data. Two pairs and several transient individuals of the Worm-eating Warbler (*Helmitheros vermivorus*), a species intolerant of forest fragmentation (Whitcomb et al. 1981, Tables 8–11), were observed only in deep forest more than 250 m from the corridor.

DISCUSSION

About 10 of the 13 or so bird species that have been shown to decline in forest fragments or show low tolerance to forest fragmentation (Bond 1957, Whitcomb et al. 1981) occurred in my study plots. Of these only the Ovenbird and Acadian Flycatcher appeared to be negatively affected by the presence of edge. The negative response of Ovenbirds to edge may help explain why this species is unable to persist even in forest islands that are much larger than its minimum territorial size (Galli et al. 1976, Forman et al. 1976, Whitcomb et al. 1981:166). Whitcomb et al. (1981: 166, 172) mention that the Worm-eating, Black-and-white, Kentucky, and Hooded warblers were also scarce in the vicinity of forest margins and may thus require forest islands considerably larger than their minimum territorial size. Of these species in my study, only the Kentucky (Fig. 2d) and Worm-eating warblers showed any indication of being less abundant near edge.

Other species that may be sensitive to forest fragmentation but which did not indicate a negative response to edges in my study include the Hairy Woodpecker, Blue-gray Gnatcatcher, Yellow-billed Cuckoo, Wood Thrush, and Scarlet Tanager (Whitcomb et al. 1981, Tables 8–11). These species' responses to forest fragmentation may therefore depend primarily on forest island size, island isolation, and other factors rather than on the effects of edge.

Cardinals, Summer Tanagers, and towhees were denser at the edges and apparently benefit from edges. However, making a conclusion on the value of edges to the cardinal and tanager is hampered by the additional occurrence of these species in the forest interior in this study as well as in other studies (e.g., Johnston and Odum 1956).

High levels of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Gates and Gysel 1978, Brittingham and Temple 1983) and predation (Gates and Gysel 1978) near edges are possible mechanisms for causing negative responses of bird density to edges. However, the relatively brief

existences, in the evolutionary time scale, of cowbird abundance in the eastern United States (Brittingham and Temple 1983) and of narrow man-made edges (Gates and Gysel 1978) suggest that other factors such as structural cues of vegetation were responsible for the observed negative responses of Acadian Flycatchers and Ovenbirds.

SUMMARY

Four breeding bird censuses were conducted with the territory-mapping method in two rectangular forested plots adjacent to power-line corridors in eastern Tennessee. The plots were subdivided into 20 or more strip transects parallel to the corridors. Density was estimated for each transect and plotted on distance from the corridor/forest edge. Plots for 22 bird species are presented. The plots were often characterized by distinct peaks and lows, indicating that territories tended to line up in rows parallel to the edge. The Acadian Flycatcher and Ovenbird were significantly denser ($P < 0.05$, 0.01, respectively) in forest interior. The Summer Tanager, cardinal, and towhee were denser ($P < 0.05$, 0.01, and 0.05, respectively) near the edge. Densities of the other species were not significantly associated with distance from the edge ($P > 0.05$).

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BREEDING BIRD POPULATIONS IN RELATION TO CHANGING FOREST STRUCTURE FOLLOWING FIRE EXCLUSION: A 15-YEAR STUDY

R. Todd Engstrom, Robert L. Crawford, and W. Wilson Baker

Most studies of avian response to plant succession document bird communities in seral habitats from open field to regional "climax" forest during a period of a few years (Kendeigh 1948, Odum 1950, Johnston and Odum 1956, Shugart and James 1973). Long-term studies of bird communities at one site as the plant community changed in secondary succession are rare (Lanyon 1981, Kendeigh 1982), and other types of succession are seldom considered. A different type of plant succession, from pine to hardwood forest, can occur in the southeastern United States depending on the frequency of fire.

Longleaf pine (*Pinus palustris*) has dominated upland coastal plain forests of the southeastern United States in historic times (Wahlenberg 1946). Fire is a major factor influencing reproduction and maintenance of longleaf pine (Christensen 1981). Fire supresses hardwood growth and removes vegetation thereby exposing bare soil which favors germination of pine seeds. Lightning-started fires formerly burned upland pinewoods over large areas but most burning is now controlled by man.

Frequent fires in pinewoods maintain an open habitat with abundant ground cover of grasses and forbs. The few remaining sections of undisturbed longleaf pine forest which have been burned annually are virtually longleaf monocultures. Along bluffs, ravines, and moist slopes where fire rarely penetrates, American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) dominate hardwood forests (Delcourt and Delcourt 1977). Beech-magnolia forests with high tree species diversity, subcanopies, and tree-fall gaps, are structurally complex compared to longleaf pine forest. These two forest communities can be thought of as opposite ends of a fire to no-fire continuum in upland areas of the southeastern United States.

Succession to pine forest following agricultural disturbance can be maintained by the presence of frequent fires. Although tree and herbaceous species of oldfield pine forest are different from those found in virgin longleaf pine forest, the abundant ground cover, openness of the habitat, and domination by pines are similar.

We report the results of a 15-year study of the breeding bird community on an 8.6-ha grid of oldfield pineland in northwestern Florida, after fire

FIG. 1. NB66 photographed from the same point in March of 1967 (top) and 1981 (bottom); "a" locates the same tree in each view.

exclusion. Bird census results and vegetation structure of a nearby mature American beech-southern magnolia forest and a relatively undisturbed longleaf pine forest are used as examples of regional old-growth communities in the presence and absence of fire, respectively. The avian communities of these two forests and 15 years of census results on the study plot are compared using rarefaction.

Nomenclature follows Kurz and Godfrey (1962) for trees.

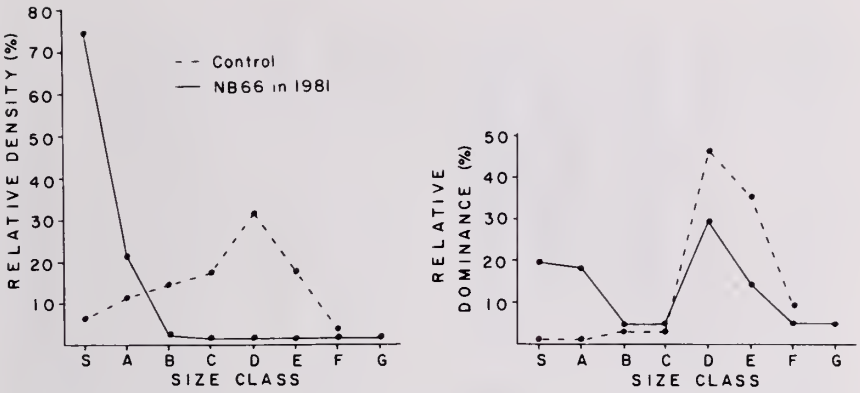


FIG. 2. Tree size class distribution within NB66 and the contiguous annually burned plot (control). Fifteen 0.04-ha circular samples were taken in each habitat.

METHODS

Study site.—In 1966 an 8.6-ha rectangular (360 × 240 m) plot was established on Tall Timbers Research Station, Leon Co., Florida, for long-term studies of plant succession and concommitant changes in bird and mammal populations. The plot was the northern portion of a south-facing slope of annually-burned oldfield pineland, in which loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*) pine were dominant. Cultivated until about 1865, some portions of the study site continued to be sharecropped until 1935 (Clewell and Komarek, unpubl.). After cessation of cultivation, pines seeded in. "Winter" (February or March) fires burned back hardwoods and shrubs giving the plot an open aspect with scattered trees and a complete ground cover of grasses and forbs. In the 15 years since fire exclusion, sapling hardwoods have grown quickly forming a thick subcanopy about 5 m tall. Photographs of the site were taken from the same perspective in 1967 and 1981 (Fig. 1). All stems >5 cm diameter breast height (DBH) were mapped in 1966 (Clewell and Komarek, unpubl.) and again in 1976 (Tobi 1977). The study plot was last burned in March 1967 and named NB66 (not burned since winter of 1966–1967). Tobi (1977) summarizes background information of the long-term NB66 study.

In 1981 vegetation was sampled within 15, 0.04-ha circular plots (James and Shugart 1970) in a stratified random design within NB66. An additional size class (S, 4–8 cm DBH) was added to the classes of James and Shugart (1970) because saplings are so numerous in NB66. Canopy cover, estimated by ocular-tube sightings, includes hardwood saplings approximately 5 m tall and pine canopy about 30 m tall.

Oldfield pinewoods contiguous with NB66 are still burned annually. Quantitative vegetation samples of these pinewoods, part of the same south-facing slope as NB66, were used to represent the vegetation structure of an annually burned oldfield pine forest. For convenience, we call this the "control" plot. Relative tree species composition (Table 1) and tree size class distribution (Fig. 2) within NB66 and the control plot are compared. Pine-hardwood density and dominance in a mature beech-magnolia forest (Woodyard Hammock) (Engstrom 1982a) and a mature longleaf pine forest (Wade Tract) (Engstrom 1982b) are contrasted to NB66 (Clewell 1981) over time (Fig. 3).

Bird censuses.—Breeding birds were censused on NB66 each spring 1967–1981 by the

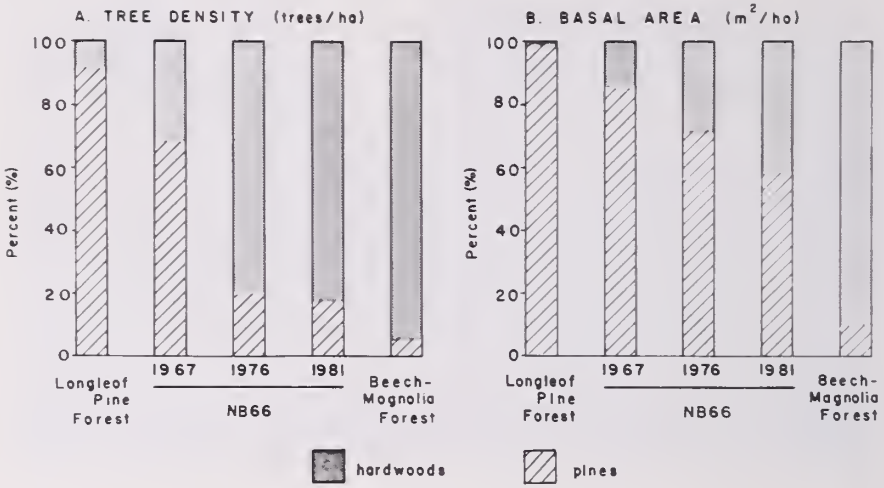


FIG. 3. Pine-hardwood density (A) and dominance (B) in NB66, a mature longleaf pine forest (Wade Tract) and a mature beech-magnolia forest (Woodyard Hammock).

spot-map method (Williams 1936). Each year, 6–11 census trips (median = 10) were made between March and June. Baker censused during 1967–1970, and 1973–1979. Crawford and Baker each completed part of the 1972 census, and Crawford censused in 1971 and during 1979–1981. Bird census results expressed as average number of detections per census trip are plotted over time (Fig. 4); acronyms for bird species (Klimkiewitz and Robbins 1978) are given in Appendix 1. Species are listed in order of year of maximum abundance and number of years observed. Numerical data are available upon request. We use average number of detections per trip instead of an estimate of the number of breeding pairs as an index of abundance, not necessarily proof of breeding. For example, Red-cockaded Woodpeckers roosted and nested within NB66 only through 1974, but individuals from a neighboring clan continued to forage in the study area until 1979. We compared average number of detections per trip to an estimate of the number of territorial individuals. In the 1982 census (not included in this paper) Crawford defined individual territories according to the spot-mapping procedure suggested by the International Bird Censusing Committee (Anon. 1970). Compared with spot-mapping, average detections overestimated abundance of three species, underestimated three species, and had equal estimates for the abundance of 20 species. Abundance in terms of mean number of detections per trip is congruous to the number of territorial pairs.

Species detected on <3 trips during any year and species not always detected in morning hours such as Red-tailed Hawk (*Buteo jamaicensis*), Chuck-will's-widow (*Caprimulgus carolinensis*), Great Horned Owl (*Bubo virginianus*), and American Crow (*Corvus brachyrhynchos*) were not included in the species total. Census trips took 1–1.5 h and were conducted in the morning before 09:30. Birds using the plot edge were excluded from censuses. "Visitors," those species having three (in years having seven or fewer visits), four (8–10 visits), and five (11 visits) detections per census year were not included in the annual species totals. This is slightly more conservative than the recommendations of the International Bird Census Committee (Anon. 1970) because of the small area of NB66.

Rarefaction.—Rarefaction is a statistical technique which can be used to compare com-

TABLE 1

RELATIVE COMPOSITION OF TREE SPECIES WITHIN NB66 AFTER 15 YEARS AND THE ADJACENT ANNUALLY BURNED PLOT (CONTROL); 15, 0.04-HA CIRCULAR SAMPLES WERE TAKEN IN EACH AREA

Species	Tree/ha		Relative density (%)		Relative dominance (%)		Frequency (%)	
	NB66	Control	NB66	Control	NB66	Control	NB66	Control
Water oak (*Quercus nigra*)	855	12	41	10	17	2	100	27
Loblolly pine (*Pinus taeda*)	257	23	12	20	28	33	93	40
Laurel oak (*Quercus hemisphaerica*)	179	2	9	1	5	<1	100	7
Sweetgum (*Liquidambar styraciflua*)	179	—	9	—	4	—	67	—
Black cherry (*Prunus serotina*)	138	2	7	1	3	<1	93	7
Flowering dogwood (*Cornus florida*)	115	8	5	7	2	<1	73	13
Shortleaf pine (*Pinus echinata*)	91	16	4	14	29	18	73	33
Sassafras (*Sassafras albidum*)	74	—	4	—	1	—	27	—
Waxmyrtle (*Myrica cerifera*)	63	—	3	—	1	—	53	—
Black tupelo (*Nyssa sylvatica*)	30	—	1	—	1	—	53	—
Pine (dead)	23	8	1	7	1	8	33	20
Post oak (*Quercus stellata*)	21	3	1	3	<1	<1	47	13
Live oak (*Quercus virginiana*)	20	2	1	1	5	<1	47	7
White oak (*Quercus alba*)	13	—	1	—	<1	—	27	—
Plum sp. (*Prunus* sp.)	13	—	1	—	<1	—	27	—
Southern red oak (*Quercus falcata*)	12	13	1	11	<1	4	20	27
Deciduous (dead)	8	—	<1	—	<1	—	20	—
Mockernut hickory (*Carya tomentosa*)	7	—	<1	—	<1	—	13	—
Longleaf pine (*Pinus palustris*)	3	26	<1	23	2	33	13	47
Tree sparkleberry (*Vaccinnium arboreum*)	2	—	<1	—	<1	—	7	—
Total	2103	115						

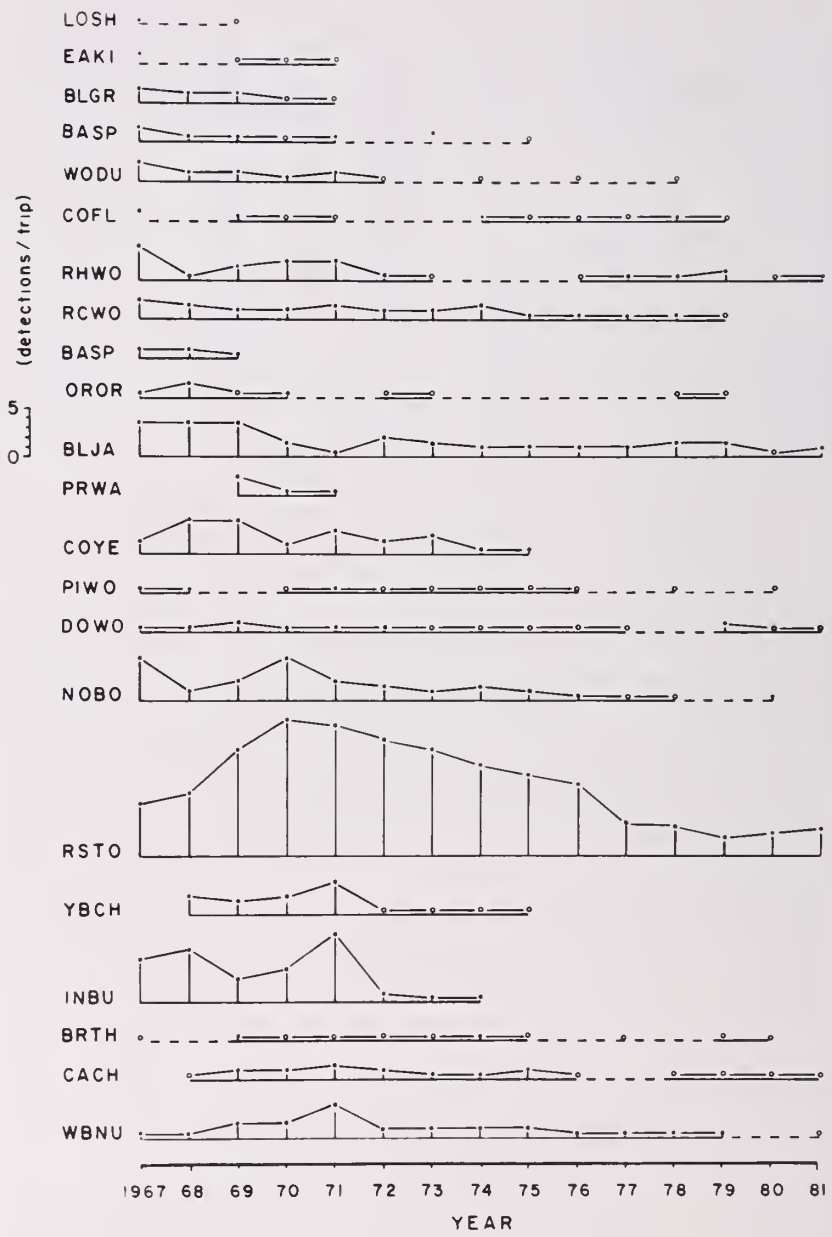
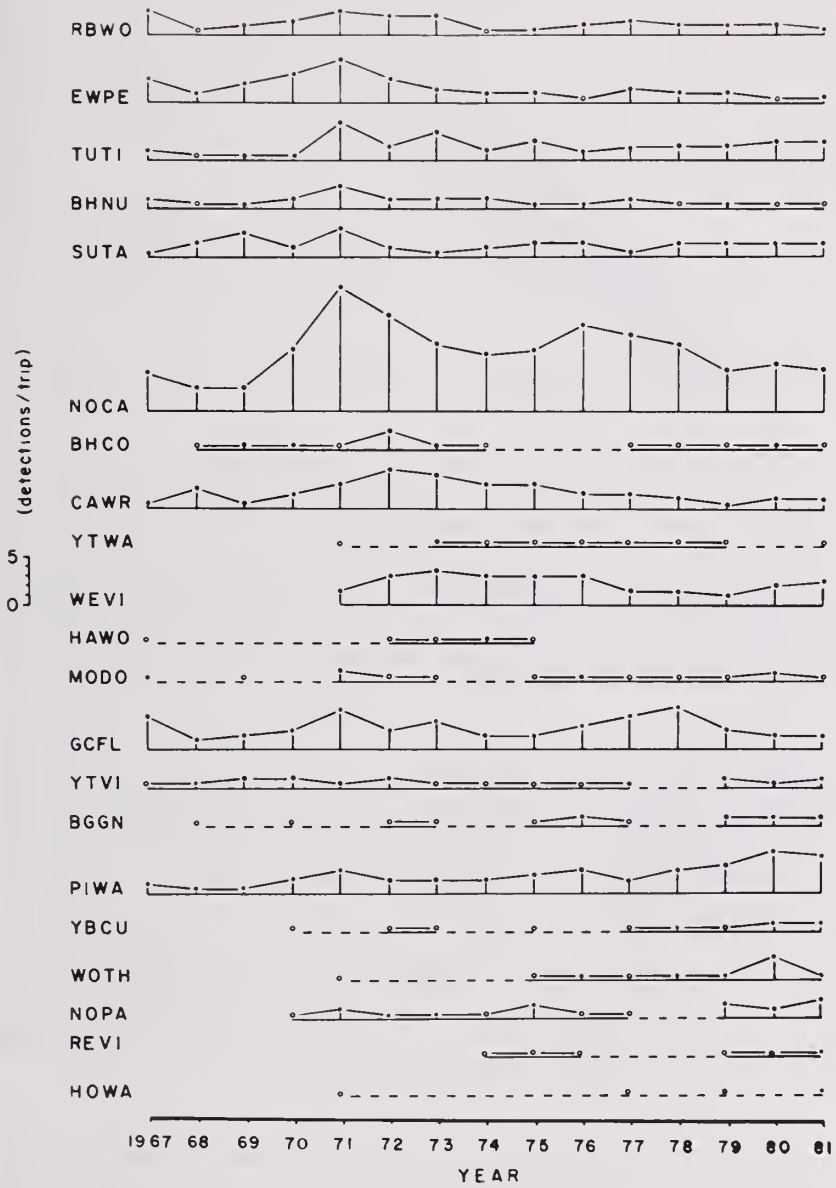


FIG. 4. Patterns of abundance in individual species over the 15-year study period. Abundance is measured in average number of detections per trip rounded to the nearest half. Open points represent "visitors" in which a species was detected only a few times during



the census year (see Methods). Species are arranged according to year of maximum abundance and number of years observed (early maxima and short duration are first in the list; late maxima and short duration are last).

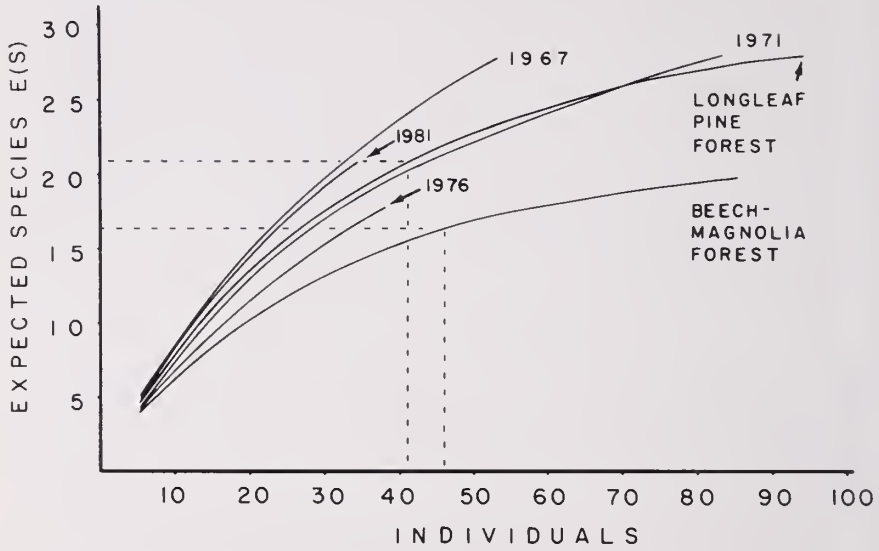


FIG. 5. Rarefaction curves for Breeding Bird Censuses of mature longleaf pine and beech-magnolia forests and selected years of NB66. Dashed lines represent the number of individuals and the expected number of species, E(S), on an 8.6-ha subplot (same size as NB66) of the mature longleaf pine (20-ha plot) and beech-magnolia (15.75-ha plot) forests.

munities with unequal sample sizes (Simberloff 1972, Heck et al. 1975). It is used here to compare number of species expected in different communities given equivalent sample area (James and Wamer 1982). In this case we compare bird species richness of three forests: a 15.75-ha mature beech-magnolia forest (Engstrom 1982a), a 20-ha mature longleaf pine forest (Engstrom 1982b), and NB66. To estimate the number of bird species expected for an 8.6-ha plot (the same size as NB66) within the larger longleaf pine and beech-magnolia forests, we first derive rarefaction curves (Fig. 5). The x-axis is the number of individuals and the y-axis is the expected number of species. End points of the curves represent the actual numbers of species (excluding visitors) and individuals found on the plots from Breeding Bird Censuses. As the sample of individuals decreases (moving toward the origin), the expected number of species declines. Assuming that the number of individuals is proportional to the area, an estimate of the number of species expected for a smaller sample of individuals (and area) than the original sample can be obtained.

RESULTS

Changes in vegetation structure over 15 years were extensive. Fire exclusion allowed sapling hardwoods (primarily water oak [*Quercus nigra*]), previously suppressed by winter fires, to grow rapidly. Comparing vegetation structure of the control plot to NB66 in 1981, canopy cover increased from 43–91% and ground cover decreased from 85–21%. Eight tree species found in NB66 in 1981 did not occur in the control (Table

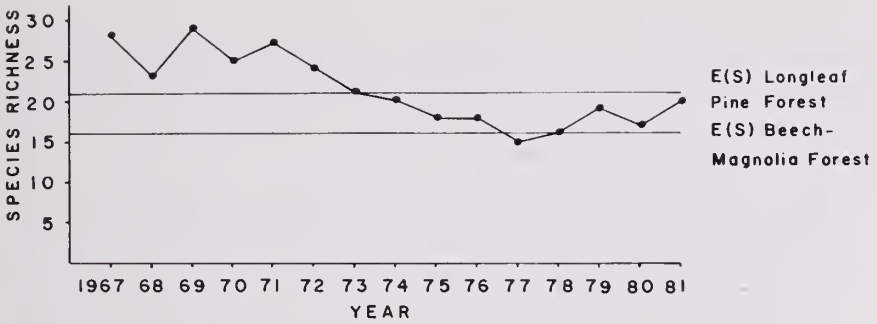


FIG. 6. The number of species within NB66 (excluding "visitors" as defined in Methods) over time compared to the number expected in an 8.6-ha sample of a mature Longleaf Pine forest (Wade Tract) and a mature beech-magnolia forest (Woodyard Hammock).

1). Density of water oaks ranged from 12 stems/ha in the control plot to 855 stems/ha in NB66, clearly showing the magnitude of structural changes occurring over 15 years (Table 1). A shift to greater density and dominance of smaller size classes is evident (Fig. 2). Relative composition of pines and hardwoods within NB66 changed markedly over time as hardwoods have become more abundant (Fig. 3).

Many deciduous trees which appeared on NB66 following fire exclusion had been present as root crowns in the annually burned forest (Tobi 1977). Root crowns send up small saplings every growing season but are burned back in winter. Hardwoods also started from seed in NB66. In February 1981, 28 American holly (*Ilex opaca*) and two southern magnolia seedlings were found within NB66 although neither species was present in 1966. These species are common in the region's mesic hardwood forests.

The bird community changed dramatically in 15 years (Fig. 4). Open habitat species (Eastern Kingbird, Loggerhead Shrike, Blue Grosbeak, and Bachman's Sparrow) disappeared within 5 years after fire exclusion. Prairie Warbler and Yellow-breasted Chat were observed for only a few years after the shrub layer began to develop (years 2–9); other species (Common Yellowthroat, Indigo Bunting, Rufous-sided Towhee, White-eyed Vireo, and Northern Cardinal) reached maximum numbers during the brushy stage (years 3–7) then slowly declined. Rufous-sided Towhee, the most abundant species for the first 8 years was not encountered in 1982. After a subcanopy of saplings developed, species associated with mesic woods (Yellow-billed Cuckoo, Wood Thrush, Red-eyed Vireo, Hooded Warbler and visitors such as Acadian Flycatcher [*Empidonax virescens*] and Kentucky Warbler [*Oporornis formosus*]) appeared in the study plot. Canopy species (Eastern Wood-Pewee, Great Crested Flycatcher, Blue Jay, and

Summer Tanager) seemed least affected by vegetation changes. Although brush encroachment has often been suggested as a cause for colony abandonment, the entire Red-cockaded Woodpecker population of Tall Timbers Research Station started to decline in 1975 (Baker 1983), so its disappearance from NB66 may have been caused by factors other than changes in vegetation structure in the colony area.

Bird species richness of mature longleaf pine forest (20-ha plot), mature beech-magnolia forest (15.75-ha plot), and the 15-year NB66 study (8.6-ha plot), compared by rarefaction, revealed that the Wade Tract contains more bird species than Woodyard Hammock (Fig. 5). In NB66 bird species abundance was greatest during the first 5 years of censusing, declined to a low in 1978, and started to increase until 1981 (Fig. 6).

DISCUSSION

Vegetation structure and species composition in the forests of northern Florida are strongly influenced by fire. Kurz (1944:78), describing vegetation changes in secondary succession following fire exclusion, emphasized the rapid sprouting of water and laurel oaks into a "phalanx of young trees" and the subsequent loss of "the undergrowth of jumbled forbs, grasses, sprouting woody plants, and interwoven vines."

The transition from an open, fire-dominated forest to a closed-canopy deciduous forest is a gradual process. Blaisdell et al. (1973) suggested that in north Florida, beech-magnolia forest will emerge in upland areas if they are not burned and are near seed sources. Although mechanisms of plant succession are complex and most generalizations must be qualified (McIntosh 1980), it is noteworthy that southern magnolia and American holly seedlings are established in NB66 as predicted (Blaisdell et al. 1973).

Wade Tract and Woodyard Hammock may be considered opposite ends of a fire/no-fire continuum, while NB66 is a community in structural transition. Tree density and species abundance are low in mature, fire-maintained pine forests compared to mesic hardwood forests (Engstrom 1982a, b). For example, in the Wade Tract, 92% of the trees are longleaf pine, whereas in Woodyard Hammock, 28 species of trees occur in addition to the dominants, American beech and southern magnolia. NB66 was an oldfield pine forest before fire exclusion, not a relatively undisturbed longleaf pine community like the Wade Tract. It was not as uniform as the Wade Tract because of past agricultural use; however, general structural characteristics of abundant ground cover, sparse canopy cover, and dominance of pines were similar.

Some studies of bird communities in relation to plant succession have shown that bird species richness increases with forest age (Johnston and Odum 1956, Shugart and James 1973). Our study is different in that we

started with a mature pine forest maintained by fire and have followed bird community changes to an early stage of a mixed pine-hardwood forest. Bond (1957) analyzed bird communities in Wisconsin in numerous wooded sites along a moisture gradient. He concluded that bird species occur in a pattern of community-types along the xeric-mesic gradient but the responses of individual species merge to changing habitat conditions in a continuum of communities. Abundance of bird species in NB66 also changed individualistically in relation to habitat structure (Fig. 4). James and Wamer (1982) compared avian species richness and vegetation characteristics of Breeding Bird Censuses reported in "American Birds." Greatest bird species richness occurred in habitats having intermediate tree species richness and canopy height. Low bird density and species richness occurred in habitats with low tree species richness, low canopy height, and high density of small trees. Lowest bird species richness within NB66 over the study period was 8–11 years after fire exclusion when oaks formed a low, dense layer beneath the pine canopy (Fig. 5). An important component of regional open-pinewoods bird communities is the ground-nesting and foraging guild which is affected adversely by decreases in grass and herbaceous cover following fire exclusion.

Coastal plain uplands in the southeastern United States were dominated historically by longleaf pine forest, whereas beech-magnolia forest was restricted to areas protected from fire (Delcourt and Delcourt 1977). Bird species richness is greater in the structurally simple longleaf pine forest than in the species rich and more structurally complex beech-magnolia forest (Figs. 5, 6). This argues against the hypothesis of greater bird species diversity with increased vertical foliage layering (MacArthur and MacArthur 1961). Greater bird species richness of the longleaf pine forest compared to the beech-magnolia forest is possibly related to the greater area of pinewoods compared to hardwoods. Palynological samples have indicated that pines have been dominant in the southeastern coastal plain over the past 5000 years (Watts 1971). More bird species could have adapted to the most common habitat, longleaf pine forest, in spite of its structural simplicity. Small plot size, greater patchiness, and more sources of food are possible reasons why more bird species occurred in NB66 than in the Wade Tract.

Of the 11 bird species observed every year of the study in NB66 (Red-bellied Woodpecker, Eastern Wood-Pewee, Great Crested Flycatcher, Blue Jay, Tufted Titmouse, Brown-headed Nuthatch, Carolina Wren, Pine Warbler, Summer Tanager, Northern Cardinal, and Rufous-sided Towhee), four species (Eastern Wood-Pewee, Brown-headed Nuthatch, Pine Warbler, and Rufous-sided Towhee) which occur regularly on the Wade Tract do not occur in Woodyard Hammock. These species may be the

next to leave NB66 permanently as the proportion of deciduous canopy increases.

Even though the pines will persist in NB66 for many years, the bird community changed significantly in the first 15 years after fire exclusion. Species nesting in ground cover quickly left the area, while birds using the high pine canopy for foraging and nesting remain in the study plot despite the hardwood growth. Species associated with mesic conditions such as Red-eyed Vireo, Wood Thrush, and Hooded Warbler are becoming increasingly common.

SUMMARY

For 15 years after fire exclusion in 1966, annual breeding bird censuses were conducted on an 8.6-ha plot of oldfield pine forest in northern Florida. Changes in vegetation structure were assessed using data from plant succession studies and by taking 0.04-ha circular samples within the study area 15 years after fire exclusion and in a contiguous annually burned oldfield forest. Using rarefaction, a statistical technique, annual bird species totals for this study are compared to bird species richness in nearby old-growth longleaf pine and mature beech-magnolia forests.

Changes in the bird community and vegetation structure were dramatic. Only 11 of 43 bird species were encountered every year of the study. Most finches and brush nesting species no longer occur on the study area while several species associated with mesic conditions have increased in abundance.

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Appendix

Scientific Names of Birds and Acronyms

Wood Duck (*Aix sponsa*)	WODU
Northern Bobwhite (*Colinus virginianus*)	NOBO
Mourning Dove (*Zenaida macroura*)	MODO
Yellow-billed Cuckoo (*Coccyzus americanus*)	YBCU
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	RHWO
Red-bellied Woodpecker (*M. carolinus*)	RBWO
Downy Woodpecker (*Picoides pubescens*)	DOWO
Hairy Woodpecker (*P. villosus*)	HAWO
Red-cockaded Woodpecker (*P. borealis*)	RCWO
Northern Flicker (*Colaptes auratus*)	NOFL
Pileated Woodpecker (*Dryocopus pileatus*)	PIWO
Eastern Wood-Pewee (*Contopus virens*)	EWPE
Great Crested Flycatcher (*Myiarchus crinitus*)	GCFL
Eastern Kingbird (*Tyrannus tyrannus*)	EAKI
Blue Jay (*Cyanocitta cristata*)	BLJA
Carolina Chickadee (*Parus carolinensis*)	CACH
Tufted Titmouse (*P. bicolor*)	TUTI
White-breasted Nuthatch (*Sitta carolinensis*)	WBNU
Brown-headed Nuthatch (*S. pusilla*)	BHNU
Carolina Wren (*Thryothorus ludovicianus*)	CAWR
Blue-gray Gnatcatcher (*Polioptila caerulea*)	BGGN
Wood Thrush (*Hylocichla mustelina*)	WOTH
Brown Thrasher (*Toxostoma rufum*)	BRTH
Loggerhead Shrike (*Lanius ludovicianus*)	LOSH
White-eyed Vireo (*Vireo griseus*)	WEVI
Yellow-throated Vireo (*V. flavifrons*)	YTVI
Red-eyed Vireo (*V. olivaceus*)	REVI
Northern Parula (*Parula americana*)	NOPA
Yellow-throated Warbler (*Dendroica dominica*)	YTWA
Pine Warbler (*D. pinus*)	PIWA
Prairie Warbler (*D. discolor*)	PRWA
Common Yellowthroat (*Geothlypis trichas*)	COYE
Hooded Warbler (*Wilsonia citrina*)	HOWA
Yellow-breasted Chat (*Icteria virens*)	YBCH
Summer Tanager (*Piranga rubra*)	SUTA
Northern Cardinal (*Cardinalis cardinalis*)	NOCA
Blue Grosbeak (*Guiraca caerulea*)	BLGR
Indigo Bunting (*Passerina cyanea*)	INBU
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	RSTO
Bachman's Sparrow (*Aimophila aestivalis*)	BASP
Field Sparrow (*Spizella pusilla*)	FISP
Brown-headed Cowbird (*Molothrus ater*)	BHCO
Orchard Oriole (*Icterus spurius*)	OROR

GENERAL NOTES

Wilson Bull., 96(3), 1984, pp. 451–456

Respiratory gas concentrations and temperatures within the burrows of three species of burrow-nesting birds.—Many species of birds nest in underground burrows. Occupants of such nests are generally protected from both predators and adverse weather conditions (Hoogland and Sherman, Ecol. Monogr. 46:33–58, 1976). However, respiratory gas concentrations within burrows may be significantly different from normal atmospheric values or those in open nests (Walsberg, Am. Zool. 20:363–372, 1980). In the burrows of the four species studied to date, oxygen and carbon dioxide concentrations are lower and higher, respectively, than normal atmospheric levels (White et al., Physiol. Zool. 51:140–154, 1978; Ackerman et al., Physiol. Zool. 53:210–221, 1980; Wickler and Marsh, Physiol. Zool. 54: 132–136, 1981; Pettit et al., Physiol. Zool. 55:162–170, 1982). The levels of carbon dioxide and oxygen encountered in burrows are known to have pronounced physiological effects on birds (Scheid, pp. 405–453 *in* Avian Biology, Vol. 6, Farner et al., eds., Academic Press, New York, New York, 1982), hence they are of particular interest. In this note we report on respiratory gas concentrations and temperatures within the burrows occupied by Rhinoceros Auklets (*Cerorhinca monocerata*), Burrowing Owls (*Athene cunicularia*), and Bank Swallows (*Riparia riparia*).

Methods.—Air temperatures and gas concentrations were measured in 26 burrows occupied by Bank Swallows in Missoula, Missoula Co., Montana during 1978, in six burrows occupied by Burrowing Owls in Payette County, Idaho, in 1980 and 1981, and in seven burrows occupied by Rhinoceros Auklets on Protection Island, Kitsap Co., Washington, in 1980. At each of these localities gas concentrations were also measured in burrows previously used by these species but unoccupied at the time.

Burrow temperatures were measured with thermistor probes (Yellow Springs Instruments) individually calibrated with a National Bureau of Standards certified thermometer. Reported temperatures are accurate within ±0.1°C.

Gas samples were withdrawn from burrows through flexible tubing (1–6 mm ID) inserted into the burrow. A volume 1.5–4 times that of the sample tube was withdrawn from the burrow and vented to the atmosphere immediately before the gas sample to be analyzed was taken. The total volume of air withdrawn from any burrow was less than 3% of the estimated burrow volume. Samples of air from Bank Swallow burrows were drawn into gas-tight 2.5-cm^3 glass syringes, sealed, and either immediately analyzed or transported to the lab for analysis. Equilibration of burrow gas samples in the syringes with the atmosphere was minimal as determined by experiments with certified gas standards. Carbon dioxide and oxygen concentrations in these samples were determined with a 0.5-cm^3 Scholander micro-gas analyzer (Scholander, J. Biol. Chem. 167:235–250, 1947). Fyrite oxygen and carbon dioxide analyzers with sample volumes of 0.5 l were used to analyze air samples from the burrows occupied by auklets and owls. The Fyrite analyzers were calibrated with gas standards whose accuracy was checked with the Scholander analyzer. Gas concentrations are accurate within ±0.05 volume percent.

The position of the temperature probes and gas sampling tubes within burrows and number and relative age of burrow occupants was confirmed by visual inspection or by excavation except in five burrows occupied by Burrowing Owls. The location and depth of these latter burrows, in addition to the nature of the soil in which they were sited, precluded their excavation.

Results and discussion.—Mean air temperatures in the burrows of these three species are

markedly different, ranging from 18.0–29.1°C (Table 1). These species differences are statistically significant ($P < 0.05$). The air temperatures within Bank Swallow burrows that are reported here are within the ranges of those previously reported (e.g., Stoner, Roosevelt Wild Life Annals 4:126–233, 1936; Ellis, Condor 84:441–443, 1982), however, the air temperatures in burrows occupied by Burrowing Owls and Rhinoceros Auklets are lower than those measured by Coulombe (Condor 73:162–176, 1971) and Richardson (Condor 53:456–473, 1961), respectively. These differences and similarities in mean air temperatures within burrows undoubtedly reflect similarities and differences in geographic location of burrows and when these measurements were made. The relatively narrow range of air temperatures (3–5°C) observed in those burrows occupied by individuals of the same species (Table 1) are indicative of the equability of the thermal microenvironment of burrows.

The mean respiratory gas concentrations in the air of burrows occupied by Rhinoceros Auklets, Burrowing Owls, and Bank Swallows are significantly different ($P < 0.05$) from those in atmospheric air (20.95% oxygen and 0.03% carbon dioxide) (Gilbert, pp. 153–176 *in* Handbook of Physiology, Respiration, Vol. 1, Fenn and Rahn, eds., American Physiological Society, Washington, D.C., 1964) and in the air of unoccupied burrows (Table 1). The oxygen and carbon dioxide concentrations in occupied Bank Swallow burrows are the most extreme of the three species studied and are statistically different at the 95% probability level from the gas concentrations in the burrows of the other two species. The mean oxygen and carbon dioxide concentrations in occupied Bank Swallow burrows are nearly 2 volume % less and more, respectively, than those, for example, in burrows occupied by auklets. Gas concentrations in the burrows occupied by Burrowing Owls are intermediate to those in occupied auklet and swallow burrows. A similar range of variation in burrow gas environments is also apparent when data available for other species' burrows are examined (Table 2). As is apparent in Table 2, burrow gas environments are either very near that of the free atmosphere or deviate considerably from atmospheric values. These variations in the composition of gas environments in burrows occupied by different species may result from differences in gas sampling or measuring techniques, but more probably result from differences in number and size of occupants, variations in soil air composition, and adequacy of burrow gas exchange or ventilation.

Despite the differences in techniques used to sample and measure respiratory gas concentrations in burrows (see Table 2 for references) the only likely source of error of this type that might yield variation of the order observed in Tables 1 and 2 concerns where air samples were collected relative to the position of the burrow occupants. Only in burrows occupied by Burrowing Owls was the proximity of the sampling tube to the occupants not assessable. Burrowing Owls were occupying abandoned badger (*Taxidea taxus*) burrows, where the nest tends to be in a side chamber off the main tunnel. Because there is a gradient in respiratory gas concentrations as one moves away from burrow inhabitants (Wilson and Kilgore, J. Theoret. Biol. 71:73–101, 1978) this architectural arrangement would usually result in samples being taken outside the nest chamber and consequently in gas concentrations lower than the real maximum for carbon dioxide and higher than the real minimum for oxygen.

Variation in the relationship between total mass of burrow occupants and nest-chamber volume probably explains much of the variation in burrow gas concentrations observed in Tables 1 and 2 (Wilson and Kilgore, 1978). The occupied Bank Swallow burrows we studied contained from 2–6 young of varying ages and in most instances usually contained an adult. In these burrows, there is a significant ($P < 0.05$) positive correlation ($r = 0.88$) between carbon dioxide concentration in burrow air and number of occupants (and therefore mass) and a significant ($P < 0.05$) negative correlation ($r = -0.89$) between oxygen concentration and number of occupants. Similar findings have been reported by Wickler and Marsh (1981). The most extreme oxygen and carbon dioxide environments in burrows of this species occur in those with 4–6 young of near fledging size where the mass to volume ratio is 0.4–0.8 g·

TABLE 1

TEMPERATURES AND RESPIRATORY GAS CONCENTRATIONS WITHIN THE BURROWS OF THREE SPECIES OF BURROW-NESTING BIRDS

Species	% oxygen			% carbon dioxide			Temperature (°C)		
	N[a]	$\bar{x}$ ± SE	Range	N	$\bar{x}$ ± SE	Range	N	$\bar{x}$ ± SE	Range
Rhinoceros Auklet									
(*Cerorhinca monocerata*)									
occupied (7)[b]	11	19.0 ± 0.2	17.0–19.8	9	1.1 ± 0.1	0.7–1.6	9	18.0 ± 0.5[d]	16.0–20.5
unoccupied (9)	8	20.3 ± 0.2[c]	19.0–20.9	5	0.6 ± 0.1[c,d]	0.3–1.0		—	—
Burrowing Owl									
(*Athene cunicularia*)									
occupied (6)	6	19.7 ± 0.2	18.9–20.3	6	1.7 ± 0.3	0.5–2.8	9	20.1 ± 0.6[d]	17.7–22.9
unoccupied (5)	3	21.0 ± 0.0[c]	21.0–21.0	5	0.2 ± 0.1[c,d]	0.0–0.5		—	—
Bank Swallow									
(*Riparia riparia*)									
occupied (26)	56	17.4 ± 0.3[e]	13.2–20.8	58	3.1 ± 0.2[e]	0.4–6.7	42	29.1 ± 0.1[d]	27.6–30.8
unoccupied (3)	7	20.6 ± 0.1[c]	20.3–21.0	7	0.4 ± 0.0[c,d]	0.2–0.5			

[a] Number of observations.
[b] Number of burrows in parentheses.
[c] Statistically different from occupied, *t*-test, $P < 0.05$ ($ts = 3.69, 2.22, 9.75, 3.05, 4.39, 11.36$).
[d] Statistically different from atmospheric air (see text), *t*-test, $0.001 < P < 0.05$ ($ts = 6.52, 3.69, 31.01$).
[e] Statistically different from other species, *F*-test and Least Significant Difference test, $P < 0.05$ ($Fs = 5.920, 7.230$).

TABLE 2

SUMMARY OF RESPIRATORY GAS CONCENTRATIONS WITHIN BIRD BURROWS

Species	% oxygen			% carbon dioxide		Reference
	N[a]	$\bar{x}$	Minimum	$\bar{x}$	Maximum	
Wedge-tailed Shearwater (*Puffinus pacificus*)	12	19.6[b]	—	0.1[b]	—	Ackerman et al. 1980
Bonin Petrel (*Pterodroma hypoleuca*)	18	19.8[b]	—	0.7[b]	—	Pettit et al. 1982
Rhinoceros Auklet (*Cerorhinca monocerata*)	7	19.0	17.0	1.1	1.6	Present study
Burrowing Owl (*Athene cunicularia*)	6	19.7	18.9	1.7	2.8	Present study
European Bee-eater (*Merops apiaster*)	20	18.2[c]	15.2[c]	3.3	6.5	White et al. 1978
Bank Swallow (*Riparia riparia*)	34	17.8	14.6	2.6	5.6	Wiekler and Marsh 1981
	26	17.4	13.2	3.1	6.7	Present study

[a] Number of burrows.
[b] Assumes a barometric pressure of 760 torr.
[c] Assumes that atmospheric air contains 20.95% oxygen.

cm^{-3}. Nest chamber volume was calculated from actual burrow dimensions assuming an ellipsoidal configuration of the nest chamber and mass of fledglings was assumed to be similar to that measured by Marsh (Physiol. Zool. 52:340–353, 1979). In contrast, the extensive nest chambers of auklet burrows (up to 9.3 l) were occupied by single chicks, 1–9 days of age; one burrow also contained an adult. The near atmospheric respiratory gas concentrations in auklet burrows, as well as those of Bonin Petrels (Pettit et al. 1982) and Wedge-tailed Shearwaters (Ackerman et al. 1980) may therefore reflect this small mass to volume ratio (mean of 0.4 $g \cdot cm^{-3}$). Mass to volume ratios were calculated from burrow dimensions and nestling masses reported by Richardson (1961).

The slopes of the relationships between increase in carbon dioxide ($\Delta\%CO_2 = \%CO_2$ in burrow $- 0.03$) and decrease in oxygen concentrations ($\Delta\%O_2 = 20.95 - \%O_2$ in burrow) in occupied burrows are indicators of the use, production, and exchange of respiratory gases within burrows. These relationships in the burrows of the three species we studied are as follows:

Rhinoceros Auklets

$$\Delta\%CO_2 = 0.86 + 0.11\Delta\%O_2 \ (N = 9;\ s_{y.x} = 0.08)$$

Burrowing Owls

$$\Delta\%CO_2 = 0.07 + 1.20\Delta\%O_2 \ (N = 6;\ s_{y.x} = 0.20)$$

Bank Swallows

$$\Delta\%CO_2 = 0.11 + 0.84\Delta\%O_2 \ (N = 55;\ s_{y.x} = 0.07)$$

Slopes that exceed the respiratory exchange ratio (carbon dioxide production/oxygen consumption) of the occupants (approximately 0.8; see Wickler and Marsh 1981) suggest that there are either additional sources for the carbon dioxide in the air of these occupied burrows, most likely from the soil, or that there is significant non-convective (i.e., diffusive) exchange of gases in these burrows. Slopes at 0.8 suggest that convective exchange (bulk flow) is the most important determinant of burrow gas composition since bulk flow of air into and out of the burrow should not alter the carbon dioxide/oxygen ratio. If the slope is less than the respiratory exchange ratio then non-convective exchange of carbon dioxide favors its loss from the burrow. The slopes of the above relationships in auklets and owls are statistically different (auklets, $t = 8.62$, $P < 0.01$; owls, $t = 2.98$, $P < 0.01$) from 0.8; however, the slope of this relationship in burrows occupied by Bank Swallows is not. Wickler and Marsh (1981) also reported a carbon dioxide to oxygen ratio of 0.86 in occupied burrows of Bank Swallows.

The relatively low levels of carbon dioxide in the burrows of Rhinoceros Auklets suggest that bulk flow of gases into and out of burrows of this species resulting from changes in barometric pressure, thermal differences between the burrow and atmospheric air, movements of occupants back and forth in the burrow acting as pistons, surface winds or passive ventilation are not relatively important, a conclusion supported by observations in Bonin Petrel burrows (Pettit et al. 1982). Presumably then, diffusive gas exchange is the primary means of burrow ventilation in these birds. Auklets, shearwaters, and petrels all construct relatively long burrows (up to 3 m); however, nest chambers in these burrows are usually within 0.5 m of the soil surface (Richardson 1961, Ackerman et al. 1980, Pettit et al. 1982). Also, the moist sandy soils in which these burrows are excavated would presumably promote the differential loss or absorption of carbon dioxide from the burrow atmosphere (Withers, Am. Nat. 112:1101–1112, 1978; Wilson and Kilgore 1978).

The accumulation of carbon dioxide in burrows occupied by Burrowing Owls as indicated by the slope of the relationship between increment in carbon dioxide and decrement in oxygen in burrows, especially considering the low levels of carbon dioxide in burrows

unoccupied by this species (Table 1), would seemingly indicate that diffusive losses of carbon dioxide from these burrows to the atmosphere are reduced.

In the burrows occupied by Bank Swallows convective means of ventilation appear to play a major role in determining the burrow gas environment. Evidence in support of this conclusion, in addition to the magnitude of the slope in the above relationship relating increases in carbon dioxide to decreases in oxygen in burrows of this species, comes from data relating burrow gas concentrations and depth of burrows. There is a positive but non-significant ($P > 0.05$) correlation ($r = 0.29$) between burrow depth and carbon dioxide concentration and a negative but non-significant ($P > 0.05$) correlation ($r = -0.26$) between depth and oxygen concentration in the burrows occupied by Bank Swallows. The same sort of relationships between gas concentration and burrow depth have been reported previously (Wickler and Marsh 1981). Interestingly, convective forms of ventilation have also been shown to be important in the burrows of the European Bee-eater (White et al. 1978).

Our data provide further evidence that the occupants of avian burrows produce and are subjected to respiratory gas environments much different from those in the free atmosphere, while the thermal regime is much buffered from that outside the burrow. The respiratory gas environments to which burrow-nesting birds are exposed are quite similar to those measured in many mammal burrows (for a review of the literature see Arieli, Comp. Biochem. Physiol. 63A:569–575, 1979; Maclean, Comp. Biochem. Physiol. 69A:373–380, 1981). Many of these fossorial mammals show a variety of physiological adjustments that help them cope with life-long exposure to low oxygen, high carbon dioxide environments (e.g., Darden, J. Comp. Physiol. 78:121–137, 1972; Ar et al., Respir. Physiol. 30:201–218, 1977; Arieli and Ar, J. Appl. Physiol. 47:1011–1017, 1979). Recent studies have revealed similar physiological adaptations in burrow dwelling birds as well (Kilgore and Birchard, Am. Zool. 20:766, 1980; Birchard and Kilgore, Physiol. Zool. 53:284–292, 1981; Boggs and Kilgore, J. Comp. Physiol. 149:527–533, 1983; Boggs et al., Comp. Biochem. Physiol. 77A:1–7, 1984).

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Sexual differences in longevity of House Sparrows at Calgary, Alberta.—The extensive body of data on survivorship of House Sparrows (*Passer domesticus*) obtained by Summers-Smith (The House Sparrow, Collins, London, England, 1963) and available from British and North American banding studies has been summarized by Dyer et al. (pp. 55–103 *in* Granivorous Birds in Ecosystems, J. Pinowski and S. C. Kendeigh, eds., Cambridge Univ. Press, Cambridge, England, 1977). In England, about 19% of House Sparrow fledglings survive to 1 year post-fledging, and annual adult survival from 1 year onward is about 50% in England and 34% in North America. Female House Sparrows have slightly higher annual survivorship than adult male House Sparrows (51% vs 45%, England; 37.3% vs 32.5%, North America; Dyer et al. 1977). Summers-Smith (1963) found that female mortality was higher than male mortality during the breeding season but the reverse obtained outside the

TABLE 1
NUMBERS OF RECOVERED HOUSE SPARROWS OF KNOWN AGE

Age (years)	No. of males	No. of females	Ratio (m/m + f)
1.0	28	23	0.55
1.5	16	13	0.55
2.0	29	33	0.47
2.5	19	9	0.68
3.0	3	1	0.75
3.5	1	0	—
4.0	6	2	0.75
4.5	2	0	—
5.5	1	0	—
6.5	1	0	—

breeding season. We monitored a large population of House Sparrows near Calgary, Alberta from 1975–1979 allowing us to evaluate sexual differences in adult survival in a harsher climatic regime than those covered by Dyer et al. (1977).

House Sparrow nestlings were banded from 1975–1978 on several farms 5–10 km E of Calgary, Alberta. Details of the study area and the House Sparrow populations can be obtained from Murphy (Condor 80:180–193, 1978; Ecology 59:1189–1199, 1978) and McGillivray (Wilson Bull. 93:196–206, 1981; Auk 100:25–32, 1983). Recoveries of banded birds were not made in a systematic way to permit formulation of a life table. Data presented here are from attempts to net all banded birds in the late autumn of 1977 and the spring of 1978. In the spring and late autumn of 1979, all recaptured birds were collected for anatomical study. A final collecting effort was made in the autumn of 1983 to recover any long-lived individuals. Hence, although our data cannot provide absolute estimates of annual adult survival, it is possible for us to examine the sex ratio of groups of survivors of known age to assess sexual differences in mortality.

Table 1 gives the number of male and female House Sparrows of known age recovered through the banding and collecting operations. All fledglings surviving to late autumn (25 October–10 November collecting dates) of their first year are assumed to be 0.5 years of age and those surviving to the following breeding season are treated as 1 year-olds even though fledging dates may range over several months. Table 1 shows that male and female sparrows have approximately equal survival to 2 years of age (ratio = no. males/[no. males + no. females] = .51, N = 142), whereas after 2 years, males are more likely to be recovered (ratio = .73, N = 45). Although it can be shown, using a test for proportions (Walpole and Myers, Probability and Statistics for Engineers and Scientists, MacMillan Publ. Co., New York, New York, 1978), that .51 is not significantly different from .5 ($Z = .24$, $P > 0.80$), whereas .73 is ($Z = 3.47$, $P < 0.001$), these tests are only descriptive since we have partitioned Table 1 into two groups arbitrarily. Nonetheless, very few females greater than 2 years old were recovered.

Lowther (Inland Bird Banding 51:23–29, 1979) documented an increased likelihood of dispersal from natal sites for female House Sparrows compared to males at Lawrence, Kansas. However, dispersal is common only among juveniles (Summers-Smith 1963; North, Ornithol. Monogr. 14:79–91, 1973; Will, Ornithol. Monogr. 14:60–78, 1973), and, if it is

a factor modifying the sex ratio of survivors, a skewed ratio should have been evident at younger as well as older adult ages given in Table 1.

Summers-Smith (Bird Study 3:265–278, 1956) attributed higher male House Sparrow overwinter mortality to predation due to a lack of vigilance on the part of the males, a trait presumably lacking in females. At a high latitude site like Calgary, winter conditions should be a greater source of mortality than would be observed in more moderate climates such as in England or throughout much of the continental U.S. (Beimborn, M.Sc. thesis, Univ. Wisconsin, Milwaukee, 1967; Cink, Ph.D. diss., Univ. Kansas, Lawrence, Kansas, 1977). Cink's (1977) autumn and winter observations at Jamestown, North Dakota indicate that males are dominant over females and should obtain better positions at feeding sites. Bumpus (Biol. Lectures, Marine Biol. Lab., Woods Hole, 1899:209–226) reported that 72 individuals in a sample of 136 House Sparrows survived a severe winter storm in Providence, Rhode Island. Fifty-one of 87 males (59%) but only 21 of 49 females (43%) survived. Mortality was not independent of sex ($\chi^2 = 3.14$, df = 1, $0.05 < P < 0.1$), suggesting that harsh winter conditions disproportionately reduce the survivorship of females.

Our observations of House Sparrows in Calgary are atypical for sexually dimorphic species and coincide with those for monomorphic species wherein males usually survive better than females, presumably because of higher reproductive costs for females (Lack, The Natural Regulation of Animal Populations, Oxford Univ. Press, London, England, 1954). The differences between our observations and those of Summers-Smith (1956, 1963) indicate that higher susceptibility of males to predation is overriden in harsh winter climates by higher vulnerability of females to severe winter conditions.

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Seed selection by juncos.—Evidence suggests that avian predators may respond to food characteristics other than, or in addition to, energy content of the items (Pulliam, Ardea 68:75–82, 1980), yet little is known of the exact determinants of diet selection (Willson, Condor 73:415–429, 1979). Investigations of food variables that influence dietary choices should be valuable in understanding foraging behavior. In the present study, we asked whether Dark-eyed Juncos (*Junco hyemalis*) select seeds on the basis of physical characteristics of the seeds, such as size, shape, and color, or on the basis of nutrient content.

Materials and methods.—Thirty juncos were captured near Fort Collins, Colorado, color banded, and maintained on 12L:12D photoperiod at room temperature in cages (25 × 25 × 25 cm) individually so that they could hear but not see each other. Age and sex were unknown. Subjects were fed a mixed diet consisting of niger thistle (*Guizotia abyssinica*) (hereafter "thistle"), canary grass (*Phalaris canariensis*) (hereafter "canary"), millet (*Panicum miliaceum*), and flax (*Linum usitatissium*). Seed and water were freely available.

TABLE 1

INDIVIDUAL PREFERENCES[a] FOR CANARY (C) AND THISTLE (T) PELLETS, DYED SEEDS, AND UNALTERED SEEDS[b]

Grams pellets				No. dyed seeds			No. unaltered seeds			
Bird	C	T	Pref.	C	T	Pref.	Bird	C	T	Pref.
Group A							Group C			
1	0.24	0.07	NP	1	83	T	1	78	99	NP
2	0.57	0.07	C	37	93	T	2	37	140	T
3	0.01	0.17	T	7	179	T	3	58	82	NP
4	0.02	0.19	T	12	76	T	4	112	71	C
5	0.01	0.19	T	1	83	T	5	86	58	NP
6	0.48	0.05	C	11	102	T	6	107	31	C
7	0.55	0.13	C	59	32	NP	7	61	104	T
8	0.52	0.05	C	61	75	NP	8	67	40	C
9	0.51	0.08	C	64	107	T	9	84	94	NP
							10	80	68	NP
Group B										
1	0.45	0.06	C	41	65	NP	1	23	66	T
2	0.41	0.03	C	52	10	C	2	56	59	NP
3	0.54	0.01	C	0	117	T	3	40	81	T
4	0.32	0.10	NP	19	165	T	4	6	155	T
5	0.48	0.01	C	78	8	C	5	34	110	T
6	0.45	0.03	C	55	22	NP	6	50	84	NP
7	0.42	0.01	C	45	68	NP	7	18	104	T
8	0.54	0.01	C	44	49	NP	8	25	97	T

[a] Preference judged by significant difference in consumption of alternative food types according to a 2-tailed *t*-test on 10 preference trials for each individual with $P < 0.05$; NP = no statistically significant preference.

[b] Tabled values for each bird are means of 10 trials.

Only canary and thistle were used in preference experiments. Ground seeds reconstituted as pellets, dyed seeds, and unaltered seeds were used in that sequence in tests. The rationale for these manipulations was that if the same preference for a food type (canary or thistle) was maintained in both seed and pellet tests, one could conclude that some nutritional component or taste was being detected by the birds and that shape, size, and handling characteristics were less important. If the birds differed in their preference for canary or thistle, depending upon the condition of the seed (e.g., pellets, dyed, unaltered), then handling characteristics or other physical properties could be considered more important.

During feeding, a junco obtained an individual seed by a pecking action then hulled the seed by rapid mandibulation while in an upright posture. While upright between pecks the individual would move its head as in scanning or shift its position slightly during the hulling activity. We interpret each peck taken during such feeding as a separate and independent action and the number of these actions as a measurement of preference when the bird was presented with alternative food types. To evaluate the possible significance of handling times for the two different seeds, we examined consumption on the basis of numbers of seeds. Therefore, we have analyzed numbers of seeds consumed, whenever possible, as a measure

TABLE 2

MEAN HANDLING TIMES (SEC) AND PREFERENCES[a] FOR CANARY (C) AND THISTLE (T) SEEDS IN DYED AND UNALTERED CONDITIONS

	Dyed seeds							Unaltered seeds		
Bird	C	T	Pref.	Bird	C	T	Pref.	C	T	Pref.
Group A				Group B						
1	10.4	6.4*	T	1	6.1	6.2	NP	9.4	5.4*	T
2	4.3	3.8	T	2	4.5	3.6	C	3.6	4.2	NP
3	5.4	3.8*	T	3	7.8	4.3*	T	7.8	4.3*	T
4	6.4	4.8*	T	4	9.0	3.7*	T	5.9	4.4*	T
5	6.4	4.5*	T	5	5.0	6.3*	C	4.0	4.8	T
6	5.1	4.9	T	6	5.9	3.7	NP	3.9	4.7	NP
7	9.3	3.2*	NP	7	4.9	5.5	NP	8.8	3.7*	T
8	3.6	3.4	NP	8	4.4	4.7	NP	3.9	4.4	T
9	4.3	4.8	T							

[a] Preference judged by significant difference in consumption of alternative food types according to 2-tailed *t*-test on 10 preference trials for each individual with $P < 0.05$ (see Table 1).

* Significantly different handling times for the two seed types shown by 2-tailed *t*-test with $P < 0.05$.

of preference. In our pellet tests we evaluated weight consumed of each food type; since the pellets, reconstituted from ground seed, were of similar size for canary and thistle, differences in weight of pellets consumed probably reflect differences in numbers of pellets consumed as well. In an independent evaluation of preferences of juncos for canary and thistle seed (Thompson et al., unpubl.), strong preference for thistle compared to canary in sequential choice tests was found; juncos selectively foraged for thistle even when seeds were presented in a ratio of four canary to one thistle and even though thistle seeds are about half the size of canary.

For simultaneous preference tests, two plastic cups approximately 3 cm diameter by 2 cm high were tacked side by side onto a small platform. Into these cups were placed paper cups approximately half full of seeds or pellets. Three groups of juncos (A = 9 birds, B = 8 birds, C = 10 birds) were studied from 16 January–4 May 1981. Three tests were conducted in the following order: (1) canary seed in pellet form vs thistle seed in pellet form; (2) dyed canary vs dyed thistle and (3) unaltered canary vs unaltered thistle. Ten separate trials of each bird were made for each type of preference test, usually on 10 consecutive days but at different times of the afternoon (most trials were made between 13:00 and 17:00). Groups A and B were used in preference tests 1 and 2, and groups B and C were used in preference test 3. An additional experiment was conducted in which birds in group C were placed either on a continuous diet of only unaltered canary or only unaltered thistle after one set of unaltered seed preference tests. Three weeks later these birds were given another set of preference tests.

For preference test 1, canary and thistle were ground separately, water was added to the powders, and the mixtures were allowed to air dry. The resulting cakes were broken into small pellets of irregular, but similar and edible, sizes. This treatment reduced handling time essentially to zero. For preference test 2, whole canary (light yellow) and whole thistle (dark grey to black) were soaked in black food dye created from a mixture of red, green, and blue, and then allowed to dry. Each experimental trial consisted of a 2-h deprivation period followed by a 1-h presentation of the two types of food. The location of a food type

TABLE 3

PERCENT OF EACH NUTRIENT COMPONENT IN CANARY AND THISTLE SEED, AND PERCENT ASSIMILATED (PARENTHESES) FOR BIRDS IN GROUP A, CALORIC VALUE OF EACH TYPE OF SEED (AND ASSIMILATED PERCENT) AND AVERAGE WEIGHTS (±1 SD) OF EACH TYPE OF SEED ARE ALSO GIVEN

	Canary	Thistle
Protein	19.53 (36.8)	19.22 (31.0)
Fat	4.51 (88.9)	20.89 (84.5)
Carbohydrates	61.61 (98.4)	15.18 (71.3)
Fiber	8.11 (82.5)	39.87 (86.7)
Ash	6.43	4.99
Calories/gm	1842 (84.3)	1124 (60.4)
Mg/seed	7.0 ± 0.02	3.1 ± 0.01

(right cup vs left cup) was alternated to control for positional effects. Similar superabundant amounts of each food type were available in the cups. The food was weighed before and after each trial with spillage poured back. Estimates of numbers of seeds eaten were derived from a regression equation for weight vs numbers of seeds. An individual's preference was judged by results of a 2-tailed *t*-test (Sokal and Rohlf, Biometry, W. H. Freeman and Co., San Francisco, 1969:330) on consumption data of the 10 trials in which the two alternative foods were presented simultaneously.

While observing each feeding bird through one-way glass, handling times for seeds were measured to the nearest 0.1 sec. Handling times were determined for groups A and B during the preference tests on dyed seed and again for group B during the preference tests on unaltered seeds. The number of measurements of handling time ranged from 10–60 ($\bar{x}$ = 25) for each bird for each kind of seed. The average number of days of experience with the seeds prior to measurements of handling time was 25 days for group A (dyed), 45 days for group B (dyed), and 55 days for group B (unaltered).

Nutrients were analyzed by Triple S Laboratories, Loveland, Colorado. We conducted a study of the assimilation of nutrient components of canary and thistle seeds by collection and analysis of feces, and this information was used in comparing preferences with nutritional value of the food items. Assimilation data were obtained by placing two groups of birds on continuous diets of either canary or thistle seed for 3 days. Each day the birds were deprived of seed from 14:00–17:00 to allow the digestive tracts to empty (Stevenson, Wilson Bull. 45:155–167, 1933; Willson and Harmeson, Condor 75:225–234, 1973), then provided with seed for 1 h, and deprived again until 07:00 the next morning. The nutrient components were determined for an amount of seed equivalent to that consumed during the hour, as well as for the feces produced from the hour of feeding. The amount of each nutrient in the fecal sample was subtracted from that in the seed consumed to find the amount assimilated.

A possible problem for studies of this kind is in finding the appropriate length of time for the post-feeding period during which feces are collected. Too short a period may not allow the digestive tract to empty, and too long a period may result in body tissues being metabolized and excreted. Our assimilation data should be valid for comparisons between our experimental groups that ate the two different types of food because the groups were treated the same otherwise, but the data may not represent absolute assimilation values.

Results.—Eliminating shape and size characteristics of the two types of seeds by grinding

TABLE 4

PROFITABILITIES OF CANARY (C) AND THISTLE (T) SEED FOR BIRDS OF GROUP A[a]

	Protein		Fat		Carbohydrate		Fiber		Calories	
Bird	C	T	C	T	C	T	C	T	C	T
1	0.06	0.04	0.03	0.09	0.47	0.06	0.05	0.18	1.21	0.35
2	0.14	0.06	0.08	0.15	1.14	0.09	0.12	0.30	2.92	0.59
3	0.11	0.06	0.06	0.15	0.91	0.09	0.10	0.30	2.33	0.59
4	0.09	0.05	0.05	0.12	0.77	0.07	0.08	0.24	1.96	0.47
5	0.09	0.05	0.05	0.13	0.77	0.08	0.09	0.25	1.96	0.50
6	0.11	0.05	0.06	0.12	0.96	0.07	0.11	0.23	2.46	0.46
7	0.06	0.07	0.04	0.18	0.53	0.11	0.06	0.36	1.35	0.70
8	0.16	0.07	0.09	0.17	1.36	0.11	0.15	0.34	3.49	0.66
9	0.13	0.05	0.08	0.12	1.14	0.07	0.13	0.24	2.92	0.47

[a] Tabled values are milligrams of nutrient assimilated per second handling time for each major component analyzed.

and feeding reconstituted pellets showed that most of the birds significantly preferred canary pellets to thistle pellets (12 canary, 3 thistle, 2 no preference, $\chi^2 = 10.7$, df = 2, $P < 0.01$, Table 1). In contrast to the results on pellets, juncos usually preferred dyed thistle to dyed canary, although many did not have a significant preference (9 thistle, 2 canary, 6 no preference, $\chi^2 = 4.5$, df = 2, $P = 0.1$, Table 1). Compared to the clear preference for canary pellets, therefore, the birds had a different preference for intact dyed seeds (G-test for independence of seed type and condition of seed, i.e., pellet or dyed, $G = 13.2$, df = 2, $P < 0.005$). We obtained results similar to those on dyed seeds when tests were performed using unaltered seeds. Juncos usually preferred unaltered thistle to unaltered canary, although many did not have a significant preference (8 thistle, 3 canary, 7 no preference, $\chi^2 = 2.3$, df = 2, $P = 0.4$, Table 1). The results on unaltered seeds indicated a different preference for unaltered seeds in comparison to the preference for canary pellets found in the first experiment (G-test for independence of seed type and condition of seed, i.e., pellets or unaltered seed, $G = 11.1$, df = 2, $P < 0.005$).

The juncos also tended to change preference to thistle over time. Group C birds (fed only unaltered thistle and canary for 3 weeks) showed the following results: at the onset of the experiment, three birds preferred canary, two preferred thistle, and five had no preference; 3 weeks later, one bird preferred canary, eight preferred thistle, and one had no preference (G-test for independence of preference trial and seed preference, $G = 7.8$, df = 2, $P < 0.025$).

Considering the dyed seeds, we found that nine birds had similar handling times for canary and thistle, and seven had significantly longer times for canary (Table 2). In only one case did a bird have a significantly longer handling time for thistle than canary. We found that seven of eight birds preferred the seed with the shorter handling time when handling times differed significantly. Five of nine birds had no preference when handling times were not significantly different for the two types of seeds. In tests involving unaltered seeds, four of four birds preferred the seed with the significantly shorter handling time and two birds with similar handling times had no preference. Thus, of the 12 juncos that had significantly different handling times for the two seeds, 11 preferred the seed (10 thistle, 1 canary), with the shortest handling time (binomial test, $P = 0.006$, Table 2). Of the 13 juncos that did not have significantly different handling times for the two seeds, seven had no preference, five preferred thistle, and one preferred canary ($\chi^2 = 4.3$, df = 2, $P = 0.1$).

To take handling time into account when considering nutritional value of a seed, we calculated the number of milligrams of each nutrient assimilated per second handling time for each seed type for birds in group A. Weight per kernel of seed was multiplied by the percent of each nutrient in the seed (Table 3). This yielded the number of grams of nutrient ingested from one kernel, which was then multiplied by the fraction which was assimilated of the nutrient in question (Table 3) to give the amount of nutrient assimilated from one kernel. Finally, the number of milligrams assimilated was divided by handling time for each individual eating that seed to give the milligrams of nutrient assimilated per second handling time, the "profitability" of a seed type.

Examination of profitability values (Table 4) shows that handling time had little effect on the nutritional value of the seeds. Profitability of canary was usually higher with respect to carbohydrate, protein, and caloric content, while profitability of thistle was usually higher for fat and fiber.

Discussion.—Canary seed was preferred when offered in the pellet form. Since differences in size, shape, and handling time of the seeds were eliminated when the pellets were formed, these could not influence choices made. Color, taste and nutritional contents were possible cues for such choices. When dyed or unaltered seeds were presented, the general preference for canary disappeared and increasing numbers of individuals preferred thistle or expressed no preference for either seed. Thus, when shape, size, and handling characteristics were returned to the seeds, preference behavior changed. Because the seeds were dyed, color is unlikely to be the basis for this change. Therefore, we conclude that physical properties such as size, shape, or hardness, which determine handling characteristics of the seeds, are important in determining preferences. This conclusion is supported by the relationships between individual preference and handling time in the majority of birds tested. Most individuals preferred the seed with the shortest handling time or had no preference when the handling times were similar. It is worth emphasizing that in spite of variation in assimilation coefficients for nutrient components of the two seeds investigated here, the same general ranking of food items obtains, canary greater than thistle, whether nutrient content of the seeds is used (Table 3) or profitabilities (Table 4).

As a final point, we observed that the juncos on the whole did not exhibit absolute preferences for a particular seed type; even though one kind of seed was strongly preferred, some of the less preferred seed was usually consumed. This result has been observed frequently in other studies and usually interpreted in terms of a sampling strategy on the part of the forager. That is, a foraging animal consumes some of a "non-optimal" diet item perhaps because this keeps options open in a setting of changing resources. Some new food may be encountered which would increase the rate of energy intake, for example. An alternative to this view is the concept of balanced diet. It may be that a small subset of the resource array available to a forager is heavily used while a diversity of other items is consumed at low levels because these rare items in the diet provide some essential nutrients. Under this concept, all-or-none selection of seeds is not expected because it does not provide a balanced diet, rather than because of sampling.

Acknowledgments.—We thank D. F. Tomback, M. A. Cunningham, A. E. M. Baker, D. B. Thompson, P. R. Sutherland, and K. Bunch for their help and advice with the study. G. B. G. gives special thanks to G. Sherman for sharing the cold sunrises while trapping juncos, and to the members of her graduate committee for their guidance: G. C. Packard, R. E. Moreng, and P. N. Lehner. Helpful comments were provided by anonymous reviewers.—GAIL B. GOLDSTEIN AND MYRON CHARLES BAKER, *Dept. Zoology, Colorado State Univ., Fort Collins, Colorado, 80523.* (Present address GBG: *150–38 Road, Flushing, New York, 11376.*) *Accepted 1 May 1984.*

Wilson Bull., 96(3), 1984, pp. 464–467

Food of Gyrfalcons at a nest on Ellesmere Island.—The Gyrfalcon (*Falco rusticolus*), our largest falcon, lives at high latitudes in a relatively impoverished environment. Several studies reporting the feeding habits of this species in Alaska and the Yukon are summarized by Sherrod (Raptor Resear. 12:49–121, 1978). Additional dietary information is available from Greenland (Hagen, Gyldendal Norsk Forlat, Oslo, 1952; Mattox et al., Arctic 25:308–311, 1972; Summers and Green, Dansk Orn. Foren. Tidsskr. 68:87–90, 1974; Fletcher and Webby, Dansk Orn. Foren. Tidsskr. 71:29–35, 1977; Jenkins, Auk 95:122–127, 1978), the United Kingdom (Bannerman, The Birds of the British Isles, Oliver and Boyd, Edinburgh and London, United Kingdom, 1956), Russia (Dementiev and Gortchakovskaya, Ibis 87: 559–565, 1945; Kistchinski, Ornithologika 1:61–75, 1958; Dementiev, Der Gerfalke, Die Neue Brehm-Bucherei, No. 264, Wittenberg, Germany, 1960), Norway (Hagen, Skr. Norske Vidensk Akad., I. Math.-Nat. Il. No. 4, 1952:1–37, 1952), Finland (Pulliainen, Ornis. Fenn. 52:19–22, 1975), and Iceland (Suetens and van Groenendael, Ardeola 12:19–44, 1966; Bengtson, Vär Fagelvärld 21:253–266, 1967; Woodin, Raptor Resear. 14:97–124, 1980). However, to date, no one has published information on the food habits of Gyrfalcons residing in the high Arctic islands of Canada (i.e., those above a latitude of 75°).

While conducting a study of the nesting behavior of a pair of white Gyrfalcons on Ellesmere Island in 1973, we had the opportunity to record the relative occurrence of various prey items in their diet. Most previous studies conclude that the Gyrfalcon is mainly ornithophagous, but the data reported here suggest otherwise for Gyrfalcons breeding in the high Arctic islands.

The eastern slopes and lowlands of Axel Heiberg Island and those of western Ellesmere Island appear richer in plant and animal life than most of the high Arctic islands. Arctic willow (*Salix arctica*) forms highly productive and extensive stands in this region. The Gyrfalcon territory we watched was in the central part of this region. The nest-site, however, was surrounded on all sides by 1.6 km or more of bleak landscape. The terrain was poorly vegetated and few birds and mammals were seen during 1973 or in previous years. Three km away from the nest lay an area of richer vegetation from which the falcons secured most of their food.

Of 23 avian species found in the region by Parmalee and MacDonald (Natl. Mus. Canada, Bull. 169, Ottawa, 1960), eight were numerous enough to be potential food for Gyrfalcons. These included Oldsquaw (*Clangula hyemalis*), Common Eider (*Somateria mollissima*), King Eider (*S. spectabilis*), Rock Ptarmigan (*Lagopus mutus*), Ruddy Turnstone (*Arenaria interpres*), European Knot (*Calidris canutus*), Long-tailed Jaeger (*Stercorarius longicaudus*) and Snow Bunting (*Plectophenax nivalis*). Among mammals, only the Arctic hare (*Lepus arcticus*), collared lemming (*Dicrostonyx groenlandicus*), and short-tailed weasel (*Mustela erminea*) could be considered as potential food for Gyrfalcons. Throughout the study period, 24-h daylight prevailed and temperatures ranged from a "night time" minimum of −6.7°C to a day time maximum of 9–10°C in still air.

On 24 May, base camp was established and four plywood observation blinds (1.2 × 1.2 × 1.8 m [L × W × H]) were placed 122 m, 366 m, 762 m, and approximately 2.5 km from the nest. A fifth blind was installed 11 m from the nest ledge on 2 July, when the young were 9 days old. The blind 366 m from the nest was occupied each day for periods ranging from a few hours to 24 h continuously. The remaining blinds were occupied sporadically and infrequently. A total of 510.5 manhours was spent watching the falcons. Prey items brought to the nest were recorded and pellets both recent and from previous breeding attempts were collected from the nest ledge, from beneath the nest, and from under perches and roosts.

TABLE 1

GYRFALCON FOODS AT A NEST ON ELLESMERE ISLAND IN THE HIGH ARCTIC AS DETERMINED FROM SIGHTINGS AND ANALYSES OF PELLETS

Species	Prey brought to the nest sightings			Pellets[a]		
	N	% occur.	% wt.	N	% occur.	% wt.
Arctic hare[b]	32	44	93.0	168	23.0	82.3
Collared lemming	7	10	0.7	298	40.8	5.1
Short-tailed weasel	3	4	1.7	2	0.3	0.2
Mammal totals	42	58	95.4	468	64.1	87.6
Ruddy Turnstone	10	14	2.3	78	10.6	3.2
European Knot	9	13	2.2	119[c]	16.2	5.2
Shorebird totals	19	27	4.5	197	26.8	8.4
Snow Bunting	0	0	0	31	4.2	0.4
Redpoll (*Acanthis flammea*)	1	1	0.1	1	0.1	<0.1
Passerine totals	1	1	0.1	32	4.3	0.4
Duck (Anatidae spp.)	0	0	0	1[d]	0.1	0.1
Rock Ptarmigan (*Lagopus mutus*)	0	0	0	14	1.9	2.9
Not identified[e]	10	14	not incl.	21	2.9	0.6[f]
Totals	72	—	—	732	—	—

[a] We examined 606 pellets.
[b] Calculated at ⅓ average adult weight.
[c] Includes three occurrences of Sanderling.
[d] Downy.
[e] Includes all other species as well as those not identified.
[f] Based on average weights of knot, turnstone, bunting, redpoll not identified to species in pelletal remains.

On 15 July, the male no longer visited the nest ledge, perhaps as a result of our intrusion. It is not known whether the male supplied food to the female out of our sight. Between 23 and 28 July, we provided pieces of hare daily as supplements to the food provided by the female for the three young. The pieces of hare left on highly visible roosting places were found and carried by the female to the nest ledge and fed to the young. In subsequent analysis of the food brought to the nest we attempted to exclude this supplemental food. Hare remains from that source did occur in pellets and probably constituted a minor bias in current year food data. Less than 10% of the total number of pellets studied appeared to have been cast during the study season, however, and only those cast during the few days of supplemental feeding could have been involved. We conclude, therefore, that the provision of hare during the study did not invalidate the overall species profile of food consumed by this Gyrfalcon family. Arctic hare not only dominated food sightings when no supplemental feeding was underway, but also dominated the contents of pellets from previous years.

We observed a total of 72 food items (exclusive of supplements) being brought to the nest, 61 of which were identified to species. A total of 606 pellets yielded 732 species occurrences. The diet contained a preponderance of Arctic hare and signficant numbers of

knots and turnstones. The genus *Calidris* formed 3.75% by weight of all food (data from pellets). All but three knots brought to the nest were the European Knot, one of which bore B. M. Band #CK68040 and was banded in Norfolk, England, on 27 August 1968. The remaining three items were Sanderlings (*Calidris alba*). Snow Buntings were not seen among any of the prey brought to the nest or in the pellets analyzed. Buntings frequented the nest ridge and were seen flying, perching, and copulating as close as 1.2 m to the sitting falcon. Old bunting nests were found in deep, wind-eroded niches in the sandstone within a few centimeters of one of the males' perches. Remains of jaeger, King Eider, and Oldsquaw were found in and near the nest, each as a single occurrence. Table 1 summarizes the results of food analysis with respect to sightings and pellets.

Early in the study, the adults fed on small young hares. Later, the adult female was observed returning to the nest with the hind quarters of larger hares, obviously flying very hard and carrying a heavy load. It appeared to be close to the maximum load that an adult female is capable of carrying in sustained flight. Once she stood for nearly a minute after landing, with drooping wings and half-open beak, panting and evidently fatigued. Pulliainen (1975) calculated a maximum carrying load of approximately 1.8 kg for Gyrfalcons.

The adults continued to bring hares to the nest as the season progressed. The young hares were usually brought to the nest only as partial carcasses, i.e., paired hind legs. They were smaller and darker in color than those young hares we saw during our daily travels. This discrepancy persisted to the end of the study, by which time young hares seen on the landscape were almost as large as adults and were white, while those brought to the nest were smaller and mostly brown.

Mammals constituted the major part of the summer diet of the Gyrfalcons we studied in 1973. Arctic hare have traditionally maintained relatively high populations in the region compared to elsewhere in the Arctic and appear to be a reliable food resource (Parker, Can. Field-Nat. 91:8–18, 1977). Late litters of hare in 1973 were numerous and accessible enough, such that the adult female could find them and bring carcasses to the nesting cliff as late as the third week of August. The Gyrfalcons were therefore able to maintain primary dependence on hares throughout the breeding season because small hares were available throughout the summer. It seems unlikely that a Gyrfalcon could kill an adult hare weighing up to 5.5 kg and certainly could not carry away even the beheaded and gutted carcass of an adult hare.

While none of Cade's (Univ. Calif. Publ. Zool. 63:151–290, 1960) data from Alaska include Arctic hare as food for Gyrfalcons, other isolated occurrences have been recorded. Bent (Life Histories of North American Birds of Prey, Pt. 2, Dover Publ., New York, New York, 1961) makes mention of it and Wynne-Edwards (Auk 69:364–366, 1952) refers to Arctic hare found beneath a Gyrfalcon nest on southern Baffin Island. Johansen (1957) and Cade (1960) stated that in western Siberia Gyrfalcons occasionally prey on snowshoe hares (*L. americanus*) and Arctic hares. Dementiev (1960) reported that Arctic hare was present in the diet of Norwegian Gyrfalcons in "small" numbers. A breeding pair of Greenland Gyrfalcons did demonstrate a reliance on Arctic hare and Snow Buntings in the absence of lemmings and ptarmigan (Summers and Green 1974). Fletcher and Webby (1977) also reported Gyrfalcon young being raised on hare.

Dementiev (Birds of the Soviet Union, Vol. 1, Engl. transl., 1951) and Cade (1960) both stated that, with regard to trophic relations, Gyrfalcons may be divided into two distinct groups: (1) the coastal and insular breeding populations feeding on aquatic birds, i.e., alcids, larids and anatids; and (2) interior populations, most of which feed predominantly on ptarmigan, even in summer. Although the Gyrfalcons in this study nested close to the sea, there were no known alcid populations in the area, the closest larid population was 48 km distant, and ducks were uncommon. Local conditions, therefore, prevented the Gyrfalcons

we watched from fitting into the feeding niches designated by Cade (1960) and Dementiev (1951) as coastal and insular.

Gyrfalcons were widely distributed throughout the high Arctic islands. Known colonies of seabirds are few and widely spaced. Ptarmigan are not known to exceed low populations there and were not observed on the project area during three previous summers. A few remains of ptarmigan in winter plumage were found near the nest but they did not amount to more than a few kills. High populations of ptarmigan have not been reported from the high Arctic islands. It therefore appears that all Gyrfalcon populations in the high Arctic do not necessarily have access to food sources regarded as typical in other areas.—Dalton Muir, *Canadian Wildlife Service, Ottawa, Ontario K1A 0E7, Canada*; and David M. Bird, *Macdonald Raptor Research Centre, Macdonald College of McGill Univ., 21,111 Lakeshore Rd., Ste-Anne-de-Bellevue, Quebec H9X 1C0, Canada.* *Accepted 10 Jan. 1984.*

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High incidence of plant material and small mammals in the autumn diet of Turkey Vultures in Virginia.—Reports of feeding behavior and food of the Turkey Vulture (*Cathartes aura*) have been mainly anecdotal (Pearson, Bird-Lore 21:319–321, 1919; Kempton, Wilson Bull. 39:142–145, 1927; Hamilton, Auk 58:254, 1941). Recent reports focus on the unusual items in the diet and behaviors associated with obtaining these foods (Jackson et al., Wilson Bull. 90:141–143, 1978; Titus and Mosher, Can. Field. Nat. 94:327–328, 1980). Materials found near nests after adults have fed young also have been used to describe the diet of Turkey Vultures (Pearson 1919; Coles, Auk 61:219–228, 1944). I examined pellets cast by Turkey Vultures to determine the dietary composition and relative frequency of food types used by these birds in the autumn.

Fifty-three pellets were collected from beneath a large roost between 28 September and 9 November 1978. The roost is located on the Radford Army Ammunition Plant, 14 km west of Blacksburg, Montgomery Co., Virginia, and was previously described by Prather et al. (Wilson Bull. 88:667–668, 1976). Pellets were air dried, weighed, and dissected. All non-hair material was removed, identified, and counted. Hair was spread over a grid and a random sample of 500 hairs was removed from each pellet and microscopically identified. Dichotomous keys (Williams, J. Wildl. Manage. 2:239–250, 1938; Mathiak, J. Wildl. Manage. 2:251–269, 1938; Spires, M.Sc. thesis, VPI&SU, Blacksburg, Virginia, 1973) and a regional reference collection were used to identify the mammal hairs. I determined the presence-absence of each mammal based on the identification of its hair in samples from all pellets. Quantification of non-mammal species was also based on presence-absence in all pellets. The proportion of species' remains in each pellet does not necessarily reflect the importance of that species in the diet of Turkey Vultures since remains of different types and of different taxa are ingested at unequal rates. The data do, however, give some suggestion of the relative abundance of various food sources.

Pellets were oblong and tapered at one end. Each measured approximately 5 cm long, 3 cm wide, and 2 cm deep at the thickest part. The mean dry weight was 2.76 ± 2.17 g. The pellets were stained with a yellow-green substance and produced a pungent odor which dissipated when they were soaked in water. Most of the pellets (74%) were composed of compacted quantities of hair or other material from one species. Incorporated into most of the pellets comprised of hair were varying amounts of vegetation, feathers, snake scutes, and a small quantity of bone.

The results reflect the diverse diet of a scavenger and are not totally unexpected (Table

TABLE 1

FREQUENCY OF OCCURRENCE OF MATERIALS INDICATING FOOD ITEMS IN 53 TURKEY VULTURE PELLETS

Non-mammal	%	Mammalian-domestic	%	Mammalian-native	%
Feathers (*Gallus gallus* primarily but not exclusively)	70	Dog (*Canis familiaris*)	26	Southern opossum (*Didelphis marsupialis*)	51
Snake scutes	4	Cat (*Felis catus*)	15	Shrew (Soricidae)[a]	23
Plant material	26	Horse (*Equus caballus*)	28	Mole (Talpidae)[a]	27
Bone	trace	Pig (*Sus scrofa*)	9	Raccoon (*Procyon lotor*)	6
		Cow (*Bos taurus*)	15	Skunk (Mustelidae)[a]	26
		Sheep (*Orvis aries*)	55	Fox (Canidae)[a]	8
				Woodchuck (*Marmota monax*)	9
				Squirrel (*Sciurus* sp.)	6
				Muskrat (*Ondatra zibethica*)	6
				Eastern cottontail (*Sylvilagus floridanus*)	19
				White-tailed deer (*Odocoileus virginianus*)	32

[a] More than one species in the family present, each with different genus.

1). Percent occurrence values ranged from a high of 70% for feathers to a low of 6% for the hairs of forest-dwelling mammals. Only feathers, and sheep and opossum remains were found to occur in more than 26 of the pellets (50%), suggesting that Turkey Vultures regularly find carcasses of these species. The feathers were primarily from chickens. A few pellets contained what appeared to be vulture feathers. Some pellets contained feathers which could not be identified to species. In approximately 70% of the pellets there was hair, feathers, or other material which could not be identified to species of origin. It would appear during the autumn that this group of Turkey Vultures ingests chicken remains more often than other types of food.

Past studies have not mentioned Turkey Vultures commonly ingesting vegetation or mole and shrew remains. Each of these less common food types occurred in approximately 25% of the pellets. Fourteen of the pellets contained some plant material which could not be identified to species, but appeared to be herbaceous. In six of the pellets plant material comprised more than one-half of the contents. Small amounts of plant material in pellets might be attributed to accidental ingestion while feeding on a carcass. However, a pellet comprised of nearly 70% plant material suggests more than accidental ingestion. Koford (Natl. Audubon Soc. Resear. Rept. 4:1–154, 1966) stated that California Condors (*Gymnogyps californianus*) ate grass and cast the undigested material. McIlhenny (Auk 56:472–474, 1939) mentioned that Black Vultures (*Coragyps atratus*) ingested cow excrement, which might have served as a source of vegetation, but gave no indication that Turkey Vultures did this. Bent (Smithson. Inst. Bull. 167:12–28, 1937) and Brown and Amadon (Eagles, Hawks, and Falcons of the World, McGraw Hill, New York, New York, 1968) have both suggested that Turkey Vultures eat rotting fruit and vegetation on rare occasions.

The frequency of mole and shrew hairs in the pellets indicate that during the autumn this group of Turkey Vultures is regularly ingesting these species. The regular ingestion of moles and shrews seems unusual because of their small size and the potential difficulty Turkey Vultures might have locating a small carcass. However, Brown and Amadon (1968) mentioned that the ability of Turkey Vultures to find bits of food in dense vegetation was "fabulous." These data support their belief that Turkey Vultures are skillful at finding small food items.

These data were based on pellets obtained from vultures in southwestern Virginia. Although the composition of the diet may not reflect the types of autumn foods used by these birds throughout their range, it does confirm that vultures eat a wide variety of items during this time of year.

Acknowledgments.—I thank the Radford Army Ammunition Plant for access to their property. I am grateful to J. Mosher, R. C. Banks, and M. W. Collopy for reviewing the manuscript.—Robert L. Paterson, Jr., *1317E-61 St., Tacoma, Washington 98404.* *Accepted 16 Dec. 1983.*

Wilson Bull., 96(3), 1984, pp. 469–470

Osprey preys on Canada Goose gosling.—At 08:00, 19 May 1983, while working at the Pratt Fish Hatchery in Pratt Co., Kansas, I observed an Osprey (*Pandion haliaetus*) dive from a 20-m hover over a pond 50 m north of my location. A pond dike blocked my view of the lower portion of the bird's descent. The osprey remained out of sight for approximately 4–5 sec before flying back into view carrying a bird in its talons. The Osprey circled over ponds to the west before landing on a large, dead cottonwood (*Populus deltoides*) on a river bank approximately 70 m north of where the attack took place.

I observed the Osprey and its prey through 7 × 35 binoculars, and, after moving to within

25 m of the perch, identified the prey as a Canada Goose (*Branta canadensis*) gosling. The gosling was flapping its wings as the Osprey began to tear pieces of flesh from the gosling's back. Observation was continued for 5 min. Consumption of the gosling continued through this time. At the attack site, I found two adult Canada Geese and three, 2-week-old goslings near the waters edge.

An Osprey had been seen catching fish at the hatchery for 5 weeks prior to the attack. In addition to fish production at the hatchery large Canada Geese are also reared in hopes of establishing a resident flock in Kansas. During the spring of 1983 65 goslings were hatched at the fish hatchery. Only two gosling mortalities were recorded the entire spring. One, as described, was the result of Osprey predation. The cause of the second mortality was unknown.

Canada Geese at the hatchery do not react to the Osprey's presence in a noticeable manner (T. Dorzab, pers. comm.). With an abundance of fish in the shallow culture ponds and in the adjacent river, it is puzzling that the Osprey preyed upon the gosling.

Ospreys occasionally catch prey other than fish (Wiley and Lohrer, Wilson Bull. 85:468–470, 1973). Bert (U.S. Natl. Mus. Bull. 167, 1937) describes the lining of nests with various items including the wings and parts of shorebirds and waterfowl. I could find no references to Osprey predation on Canada Geese goslings in the literature.—William G. Layher, *Environmental Services, Kansas Fish and Game Commission, RR #2, Box 54A, Pratt, Kansas 67124.* *Accepted 23 May 1984.*

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Pellet casting by Common Grackles.—While conducting field tests in central Tennessee during the winter of 1982–83, I noted numerous cylindrical, pellet-shaped masses among the accumulated guano deposits in blackbird (Icterinae)-starling (*Sturnus vulgaris*) roosts. These 'pellets' appeared to have been 'cast' or regurgitated. They were composed primarily of corn hulls and chaff, and contained no discernible guano. Based on the size of these pellets (about 1 cm in diameter and 1–3 cm in length) and the species composition of these roosts, I assumed they were produced by Common Grackles (*Quiscalus quiscula*). This assumption was later supported when captive grackles, fed cracked corn, produced similar pellets. European Starlings held in captivity at the same time, failed to produce these pellets. Conversely, captive Brown-headed Cowbirds (*Molothrus ater*) produced a similar, albeit considerably smaller (5 × 7 mm) pellet, when fed a mixed corn and poultry mash diet. Hansen (Internatl. Bird Pellet Study Group, Bull. No. 7, 1977; G. E. Duke, pers. comm.) found that Shiny Cowbirds (*Molothrus bonariensis*) cast similar pellets. Whether Red-winged Blackbirds (*Agelaius phoeniceus*) produce similar pellets is not known. However, since red-wings and cowbirds represented only a small proportion of the bird population at the roosts containing these pellets, it is doubtful they contributed significantly to their deposition.

To obtain a rough estimate of the number of these pellets produced, a total of 30, 0.5 m^2-paper plots were randomly placed within a 1.2-ha roost of small (3–5 m) hardwoods near Lawrenceburg, Lawrence Co., Tennessee. Ten plots were placed on each of the evenings of 8, 14, and 15 February 1983, collected the following morning, and the number of pellets deposited during the night enumerated. This roost had an estimated bird population of 0.6–0.8 million birds, comprised of an estimated 61% grackles, 35% European Starlings, 3% Red-winged Blackbirds, and 1% cowbirds. Therefore, the estimated density of grackles in this roost was between 31 and 41 grackles/m^2.

The number ($\bar{x} \pm$ SE) of pellets cast per evening at this roost was estimated at 5.2 ± 0.8 pellets/m^2 for an estimated total of 62,400 pellets. Although the number of these pellets per plot ranged from 0–11, probably varying with the bird density within the site, the rate of deposition did not vary significantly ($F = 0.40$, $P = 0.67$) among the three nights.

Ten randomly selected pellets were fragmented and their composition by volume estimated by a random plot method (Dolbeer et al., Wilson Bull. 90:31–44, 1978) to include 90% hulls, chaff, and other vegetable residue (primarily corn), 5% rock, 4% insect exoskeletons, and 1% bone and shell.

Pellet casting has been well summarized for raptors by Duke et al. (Comp. Biochem. Physiol. 53A:1–6, 1976) and has been reported for several other species including: Northwestern Crows (*Corvus caurinus*) (Butler, Can. Field-Nat. 88:313–316, 1974) and Killdeer (*Charadrius vociferus*) (DeVlaming, Wilson Bull. 79:449–450, 1967). Additionally, Warham (Emu 57:78–81, 1957) collected pellets cast by Splendid Blue Wrens (*Malurus splendens*) from beneath their roosting site. However, to the best of my knowledge, this is the first reported observation and quantification of pellets cast by Common Grackles.—Daniel J. Twedt, *U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Kentucky Research Station, 334 15th Street, Bowling Green, Kentucky 42101.* *Accepted 28 Mar. 1984.*

Wilson Bull., 96(3), 1984, pp. 471–477

Preflight behavior of Sandhill Cranes.—The purpose of this paper is to describe and quantify preflight behavior of Sandhill Cranes (*Grus canadensis*), including the exit of cranes from overnight roost sites. Preflight behaviors are social signals that convey information from one individual or group to another (Heymer, Ethological Dictionary, Garland Publ. Inc., New York, New York, 1977), and understanding the preflight behavior of Sandhill Cranes may assist in interpretation of social organization.

Methods.—Preflight behavior of Sandhill Cranes was studied from early January through February 1978–1980 near Rich Lake, Terry Co., Texas; during March and early April 1978–1980 along the Platte River between Sutherland and North Platte in Lincoln Co., Nebraska; during the last 2 weeks of April 1980 near the north end of Last Mountain Lake, Saskatchewan; during May 1980 near Delta Junction, Alaska; and immediately prior to nesting in May 1980 near Old Chevak, Clarance Rhode National Wildlife Refuge, Alaska.

Observations were aided by a 15 × 60 telescope. Postures and movements were photographed (35 mm) and filmed (16 mm). Descriptions and social interactions were recorded on tape during 1109 observation periods totaling 369.7 h. Behaviors were recorded continuously for 20 min during these observation periods using behavioral categories defined in this paper (preflight behaviors) and elsewhere (Tacha, Ph.D. diss., Oklahoma State Univ., Stillwater, Oklahoma, 1981).

Juvenile (young-of-the-year) cranes were distinguished from adults by brown feathering on the nape (Lewis, J. Wildl. Manage. 43:211–214, 1979). Sex of some cranes was determined in the field by observation of the unison call (Archibald, Ph.D. diss., Cornell Univ., Ithaca, New York, 1975). Sex was determined during 54 of the observation periods when both members of a pair were present, by assuming that females follow males. None of these sex identifications was found to be incorrect when unison calls were subsequently observed. Observation of one crane of a pair following another was used to designate sex during some observation periods in which the unison call was not observed. Pairs (two adults) and family units (two adults and one or two juveniles) were identified by their close proximity (compared to other cranes in larger flocks); the tendency was for adult females of pairs to follow the

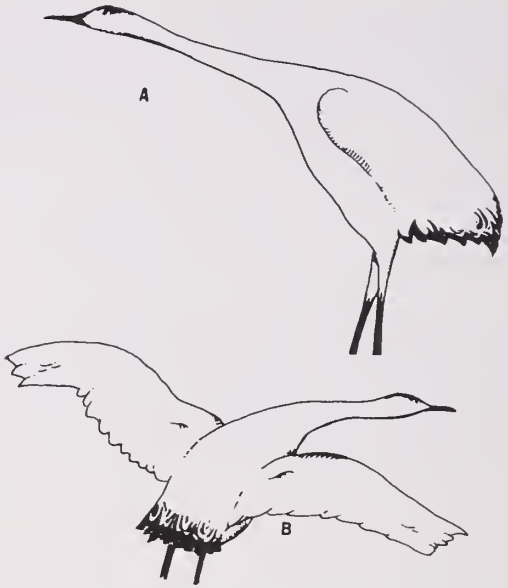

FIG. 1. Neck stretch (A) and neck stretch-wings-spread (B) preflight signals of Sandhill Cranes (A from 35 mm slides, B from 16 mm films).

male, and juveniles of family units to follow their parents. The sex of juveniles could not be determined in the field, and no juveniles were ever observed to be members of a mated pair. The sex of adults not in pairs or family units could not be determined.

When behavioral observations were transcribed from tapes, the durations of behaviors were rounded to the nearest full second. Cranes were selected for observation using stratified random sampling as follows: observations were obtained in all major habitats used by cranes at all hours of the day; sampling was stratified by age groups to ensure adequate sampling

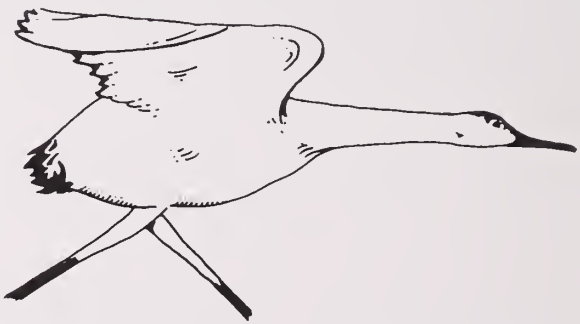

FIG. 2. The neck stretch-wings-spread-run preflight signal of Sandhill Cranes (from 35 mm slides).

TABLE 1

PERCENTAGE OCCURRENCE OF PREFLIGHT SIGNALS IN TIME BUDGETS OF SANDHILL CRANES

Age/sex/social status	N	$\bar{x}$ %	Z	P
Adult	1050	6.19	0.76	0.45
Juvenile		5.01		
Male	291	8.00	0.78	0.43
Female		5.67		
Adults[a]				
Alone	365	7.81	0.41[b]	0.81
Pair		6.67		
Family		5.26		
Juveniles[a]				
Alone	272	6.45	1.09	0.27
Family		3.33		
Males[a]				
Pair	90	7.04	0.28	0.78
Family		5.26		
Females[a]				
Pair	118	6.98	0.79	0.43
Family		3.13		

[a] Data for time budgets on cranes of known social status.
[b] χ^2 value.

of juveniles; and cranes which had been marked (neck collar and leg band) for fewer than 7 days were not sampled. Three methods of quantifying preflight behaviors were used: frequency of occurrence of behaviors using each observation period as an experimental unit; duration of each behavior using each observation of the behavior as the experimental unit; and the percentage of total time spent in each behavior using observation periods as the experimental units. Results were considered to be statistically significant when $P < 0.05$.

Stepwise multiple regression was used to evaluate the association between frequency of occurrence of preflight signals and various environmental variables. The initial model used seven classification variables (each variable had two or more class levels) including period of the year, hour of the day, habitat, general flock activity, flock size (seven levels), and year. Non-significant variables were removed one at a time, in descending order of the *P*-level for their partial sums of squares.

Preflight intention movements.—Preflight intention movements were divided into two categories based on their presumed message content following Smith (Science 165:145–150, 1969). The first category, signaling "I may fly soon" sometimes led to the second category, "I am going to fly," if the stimulus persisted. The second category did not necessarily need an external stimulus; motivation to change location appeared sufficient.

The two displays that signaled "I may fly soon" were wing flapping (Tacha 1981) and leaping into the air with wings outspread and flapping. Wing flapping also often resulted in activities other than flight. Leaping with wings flapping had a higher stimulus threshold and led to flight if the stimulus (usually danger) approached or persisted. Wing flapping and

TABLE 2

PERCENTAGE OF TIME SANDHILL CRANES SPENT EXHIBITING PREFLIGHT SIGNALS

Age/sex/social status	N	$\bar{x}$ %	SE	*t*	*P*
Adults	711	0.074	0.021	0.01	0.99
Juveniles	339	0.074	0.027		
Males	150	0.007	0.031	0.57[a]	0.57
Females	141	0.116	0.083		
Adults					
Alone	128	0.131			
Pair	180	0.102	0.545[b]	0.11[c]	0.090
Family	57	0.080			
Juveniles					
Alone	62	0.117	0.074		
Family	210	0.013	0.006		
Males					
Pair	71	0.038	0.019	0.27	0.79
Family	19	0.053	0.053		
Females					
Pair	86	0.170	0.135	1.11[a]	0.27
Family	32	0.018	0.018		

[a] Unequal variances, $P < 0.05$.
[b] ANOVA error mean square $\times 10^{-4}$.
[c] ANOVA *F*-value.

leaping with wings flapping were observed only twice during observation periods in a preflight context, and were considered displacement activities resulting from conflicting motivations to depart or to stay.

Sandhill Cranes exhibited a stereotyped preflight intention display that signaled "I am going to fly." This neck-stretch display had three distinct intensities (Figs. 1a, b, 2). The simple neck-stretch display consisted of a crane standing on both legs and arching the neck foward. The body was held upright at about 20–30° above horizontal with wings folded. The orientation of the bill indicated the direction of intended takeoff.

The function of the neck-stretch display may be to elicit other cranes of a pair or family to take flight with the displaying bird. If the simple neck-stretch display did not provoke signal receivers into flight, the next highest intensity of display was employed. The simple neck-stretch was augmented by fully or partially spreading the wings (Fig. 1b). The displaying crane would turn its head, presumably to observe the response of intended signal receivers. If no response occurred, the third level display was employed by running for a short distance with neck stretched forward and wings outspread (Fig. 2).

Forty-nine of the 54 neck-stretch signals observed resulted in flight; the five exceptions occurred when juveniles exhibited the simple neck-stretch. The neck-stretch-wings-spread display preceded flight each of the five times it was observed. The neck-stretch-wings-spread-run was exhibited only twice and led to flight both times.

Frightened cranes went directly to the neck-stretch-wings-spread-run while uttering an

TABLE 3

FREQUENCY OF OCCURRENCE OF PREFLIGHT SIGNALS IN TIME BUDGETS USING SIGNIFICANT VARIABLES FROM REGRESSION ANALYSIS[a]

Habitat	N	$\bar{x}$	DMRT[b]	Location	N	$\bar{x}$	DMRT[b]
Plowed	39	0.333	A	AK-DJ	64	0.313	A
Cotton	114	0.167	A B	TX	350	0.120	B
Native hay	91	0.165	A B	NE	457	0.077	B
Marsh	69	0.159	A B	SK	120	0.075	B
Alfalfa	122	0.107	B	AK-OC	56	0.054	B
Milo	227	0.079	B				
Corn	203	0.074	B	Year	N	$\bar{x}$	DMRT[b]
Tundra	35	0.057	B	1979	193	0.165	A
Wheat	69	0.043	B	1980	854	0.090	B
Barley-planted	18	0.000	B				
Barley-stubble	12	0.000	B				
Mixed alfalfa-hay	48	0.000	B				

[a] Regression analysis: habitat partial SS = 12.7, $F = 4.35$, OSL = 0.001; location partial SS = 12.0, $F = 11.23$, OSL = 0.001; and year partial SS = 1.1, $F = 4.19$, OSL = 0.04. Full model df = 16,1030; error mean square = 0.266; $F = 4.12$; OSL = 0.001; $R^2 = 0.06$.

[b] Duncans Multiple Range Test.

alarm call (Archibald 1975). Archibald (1975:11) described a "flight intention call" for Sandhill Cranes. I did not notice any call associated with preflight intention movements of Sandhill Cranes other than the rare alarm call.

The preflight neck-stretch or a variation occurred in 5.5% of the observation periods. No difference ($P > 0.27$) in frequency of occurrence of preflight signals (hereafter referring to the neck-stretch and its variations) was observed between age, sex or social classes of Sandhill Cranes (Table 1).

The neck-stretch display had a mean duration of 17.6 sec among adult females, 10.1 sec among juveniles, and 8.2 sec among adult males. These differences were not significant (ANOVA EMS = 126.6, df = 2.51; $F = 2.44$; $P = 0.097$). Only one adult male exhibited the neck-stretch-wings-spread display; juveniles exhibited the neck-stretch-wings-spread-run twice during observation periods. Preflight signals from adult males resulted in flight with signal receivers more quickly and more often (100%, N = 23) than preflight signals from either adult females (75%, N = 16) or juveniles (53%, N = 17). The reduced duration and high response rate to preflight signals from adult males suggests that adult males may play a leadership role in determining when to fly.

Sandhill Cranes spent an average of 0.074% of their time performing preflight intention movements (Table 2). No differences in percentage of time spent exhibiting preflight displays were observed between age, sex or social classes.

I hypothesized that frequency of preflight signals was associated with environmental variables. The best regression model (Table 3) included habitat, location, and year variables with an R^2 of only 0.06. Differences within variables suggested that higher frequencies of preflight signals were associated with the Delta Junction area of Alaska and plowed fields in Texas. Cranes flew into and out of plowed fields in Texas and the Delta Junction Alaska area more often than they did in other habitats or locations (based on marked cranes, Oklahoma Cooperative Wildlife Research Unit, unpubl.). The low R^2 from regression anal-

TABLE 4

SEQUENCES OF BEHAVIORS OF SANDHILL CRANES ON ROOSTING AREAS AFTER WAKING BUT BEFORE TAKING FLIGHT

Behavior category	Order of behaviors after waking and before flight								
	1	2	3	4	5	6	7	8	Total
Double wing stretch	15	15	1	1	0	0	0	0	32
Wing flap	3	6	7	6	8	5	2	0	35
Body shake	0	7	13	5	6	2	0	0	33
Loafing	18	5	4	6	6	5	3	0	49
Preening	2	4	9	9	3	3	3	0	33
Walking	1	2	5	4	4	2	4	0	22
Preflight	0	0	0	2	5	6	8	9	30
Total	39	39	39	33	32	23	13	9	

ysis suggested that most of the variation in use of preflight signals was not associated with variables I could measure in this study.

Departure from roosting areas.—Individual cranes were observed during the interval from when they awakened until flight from roost sites in Texas and Nebraska on 39 occasions (Table 4). Seven types of behavior (Tacha 1981) were observed during the sequences of activity characteristic of this interval. Each of the behaviors occurred only once, if at all, in each sequence, except for loafing which occurred an average of 1.26 times per sequence. The double wing-stretch was observed in 82% of the sequences, nearly always as the first or second behavior after waking. Wing flapping was observed in 90% of sequences and occurred throughout the interval. Body shakes were observed in 85% of sequences and tended to occur in the middle of a sequence. Preening was seen in 85% of roost exit sequences and throughout the order of behaviors. Walking was noted in 56% of sequences and occurred toward the middle of the order of behaviors. Preflight signals occurred in 77% of sequences and were always the terminal behavior of the sequence. A typical sequence was as follows: awaken-loafing up-double wing stretch-body shake-walking-preen-wing flapping-preflight-flight.

Members of mated pairs and families appeared to remain together in two or three bird groups during roost departure with a coordinated takeoff that resulted from preflight intention movements. Cranes without mates or young appeared to take off alone or in small (5–15 birds) groups. Once airborne, pairs, families, and unmated adults would form larger flocks as distance from the take off point increased. Cranes flying a distance of less than 2–3 km remained in an unstructured group at low altitudes. Cranes flying further than this formed long lines at right angles to the direction of flight and flew higher than 300 m.

Sandhill Cranes often formed communal roosts of as many as 100,000 birds in western Texas and Nebraska (Oklahoma Cooperative Wildlife Research Unit, unpubl.). On 12 occasions, these large aggregations of cranes flushed all at once from roost sites. On each occasion, many cranes appeared to have become separated from members of their social units. The use of preflight signals and a somewhat standardized sequence of behaviors after waking apparently allowed a coordinated takeoff of pairs and family units, limited confusion resulting from separation of these social units, and reduced potential for in-flight collision during departure of cranes from roost sites.

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Research Program for Migratory Shore and Upland Game Birds, administered by the Central Management Unit Technical Committee and the Migratory Bird and Habitat Research Laboratory, U.S. Fish and Wildlife Service. The Oklahoma Cooperative Wildlife Research Unit has Oklahoma State University, Oklahoma Department of Wildlife Conservation, U.S. Fish and Wildlife Service, and Wildlife Management Institute cooperating. I thank P. A. Vohs for his advice and manuscript review, G. C. Iverson and D. C. Martin for assistance during fieldwork, and W. D. Warde for assistance with statistical analyses.—THOMAS C. TACHA, *Cooperative Wildlife Research Unit, 404 Life Sciences West, Oklahoma State Univ., Stillwater, Oklahoma 74078.* (Present address: *Cooperative Wildlife Research Laboratory, Southern Illinois Univ., Carbondale, Illinois 62901.*) *Accepted 15 Dec. 1983.*

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Vocal mimicry of Nashville Warblers by Yellow-rumped Warblers.—Many recent studies have emphasized the importance of learning in avian song development (surveyed by Kroodsma and Baylis, pp. 311–337 *in* Acoustic Communication in Birds, Kroodsma and Miller, eds., Academic Press, New York, New York, 1982). Birds are known to discriminate among potential song tutors (Marler and Peters, Science 198:519–521, 1977; West and Stroud, Wilson Bull. 95:635–640, 1983), yet misdirected song learning does occur (Baptista and Morton, Auk 98:383–385, 1981). Among the Parulinae, interspecific vocal learning has been demonstrated for only one species, the Common Yellowthroat (*Geothlypis trichas*) (Kroodsma et al., Wilson Bull. 95:138–140, 1983). This note describes a striking similarity between the songs of some Yellow-rumped Warblers (*Dendroica coronata*) and Nashville Warblers (*Vermivora ruficapilla*) in northern Michigan, which apparently arose from misdirected song learning by Yellow-rumped Warblers.

Methods.—The study area consisted of 37 islands (0.01–20.6 ha) at the northeastern tip of Isle Royale National Park, Michigan. The vegetation on these islands is typical boreal forest (Edwards, Ph.D. diss. Univ. Michigan, Ann Arbor, Michigan, 1978). During June 1983 I recorded singing warblers using a Marante PMD 200 tape recorder and an Audiotechnica AT9100 directional microphone. Audiospectrograms of the recordings were made on a Kay Elemetrics Vibralyzer 6030-A at wide band setting (300 Hz). In this paper, a song "element" is defined as a sound that appears as an uninterrupted mark on an audiospectrogram; a series of elements of the same type is called a "phrase" (Wolffgramm and Todt, Behaviour 81:264–286, 1982). Songs of Nashville Warblers ordinarily consist of two phrases; those of Yellow-rumped Warblers consist of one to three phrases. Yellow-rumped Warblers which sing Nashville-type songs are termed "mimics" here.

I made two censuses of the breeding bird population on each island between 11 June and 12 July. The purpose was to assess the relationship between Yellow-rumped Warbler song characteristics and the abundance of singing Nashville Warblers in the immediate vicinity.

I made five measurements on each audiospectrogram: song duration (msec), maximum frequency (kHz), minimum frequency, and average time between elements within first and last phrases of the song. For Yellow-rumped Warblers with songs consisting of a single phrase, the latter two measurements were identical. These data were analyzed using Discriminant Function Analysis (Nei et al., Statistical Package for the Social Sciences, McGraw-Hill, New York, New York, 1975) to determine if the songs of typical Yellow-rumped and Nashville warblers could be distinguished by measures of frequency and tempo, and to predict the group membership of mimic Yellow-rumped Warblers by the same criteria. Two central assumptions of linear discrimination, homogeneity of variances among groups and

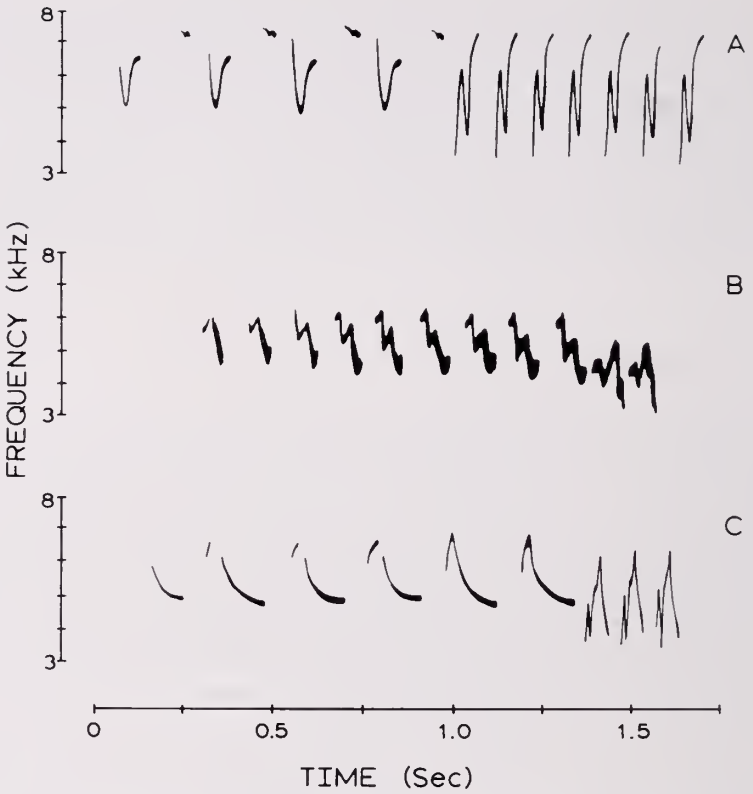

FIG. 1. Ink tracings of audiospectrograms of a typical Nashville Warbler (A), typical Yellow-rumped Warbler (B), and mimic Yellow-rumped Warbler (C). Nashville and mimic Yellow-rumped warblers differ from typical Yellow-rumped Warblers in their generally higher frequency and accelerating tempo.

normal distribution of observations, were tested with the F_{max}-test for homogeneity of variances, and the *G*-test for goodness-of-fit (Sokal and Rohlf, Biometry, Freeman, San Fransisco, California, 1981). The only violation consisted of significantly different variances between groups in the time between elements in the last phrase of the song ($F = 3.29$, $P < 0.01$). This single violation is less extreme than those in many ecological data sets used in discriminant analysis, and is not likely to have influenced the outcome of the analysis (Williams, Ecology 64:1283–1291, 1983).

I also sorted songs according to the similarity of their elements. The shape of each element was measured by the following procedure: (1) The element was divided into intervals within which the slope of the tracing was uniformly either positive or negative. For example, the elements in the last phrase of the song in Fig. 1A have three such intervals, while those in the last phrase of the song in Fig. 1B have four intervals. (2) For each interval, I measured the initial frequency, duration, and average width and slope (Hz/msec) of the mark. The width of the tracing on an audiospectrogram varies primarily with the range of frequency

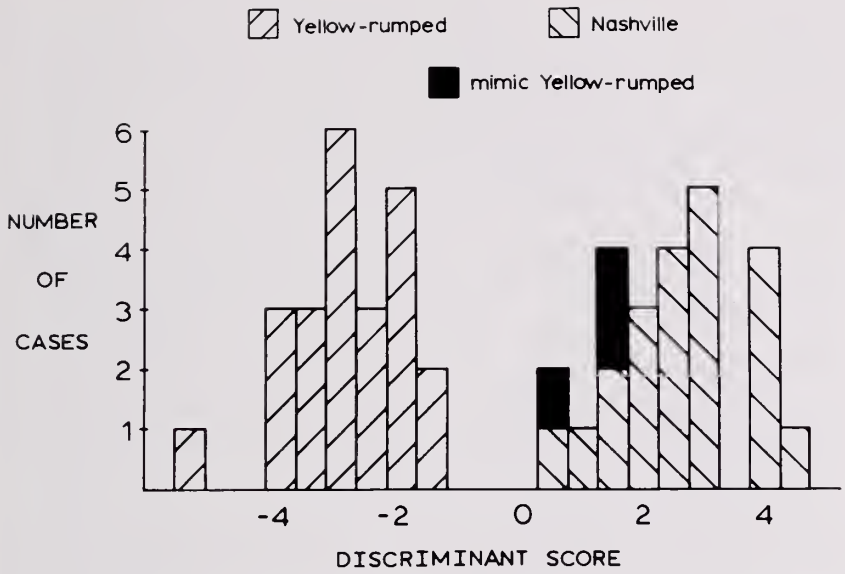

FIG. 2. Distribution of discriminant scores of warbler songs. Scores of typical Yellow-rumped and Nashville warblers do not overlap (group centroids: Yellow-rumped Warbler, −2.65; Nashville Warbler, 2.90). Mimic Yellow-rumped Warbler songs are similar to those of Nashville Warblers, according to this analysis based on five measures of frequency and tempo.

being produced. For example, the elements in Fig. 1A are narrower than those in Fig. 1B because at any one time the acoustic energy in the elements of Fig. 1A is channeled into a narrower range of frequency. The measurement error in this analysis was minimized by measuring elements with a standard procedure on a 1-mm grid. The variation due to measurement error was small compared with variation due to real differences between songs. (3) I compared elements by comparing their intervals in sequence, weighting each of the four measurements equally. Similarities between songs were then found by weighting the similarities between pairs of their elements by the number of times each element was repeated in its respective song. The resulting song similarity matrix was analyzed using cluster analysis (Davis, Statistics and Data Analysis in Geology, John Wiley, New York, New York, 1973).

Results.—Three species comprised 61% of the breeding bird population of the study area: Yellow-rumped Warbler (0.69 pairs/ha on 26 islands), Song Sparrow (*Melospiza melodia*) (0.65 pairs/ha on 32 islands), and Nashville Warbler (0.38 pairs/ha on 11 islands). I observed Yellow-rumped Warblers singing mimic songs at six sites within the study area, including at least four individuals. Based on censuses of the 37 islands, roughly 8% of the Yellow-rumped Warbler population sang mimic songs. I was able to record three of these (Fig. 1). Clear audiospectrograms were obtained for 23 additional Yellow-rumped Warblers and 21 Nashville Warblers.

Discriminant analysis using the five measures of song structure correctly classifies all typical songs according to species (Fig. 2). Mimic Yellow-rumped Warbler songs fall within the region of typical Nashville Warbler songs (associated probabilities of misclassification

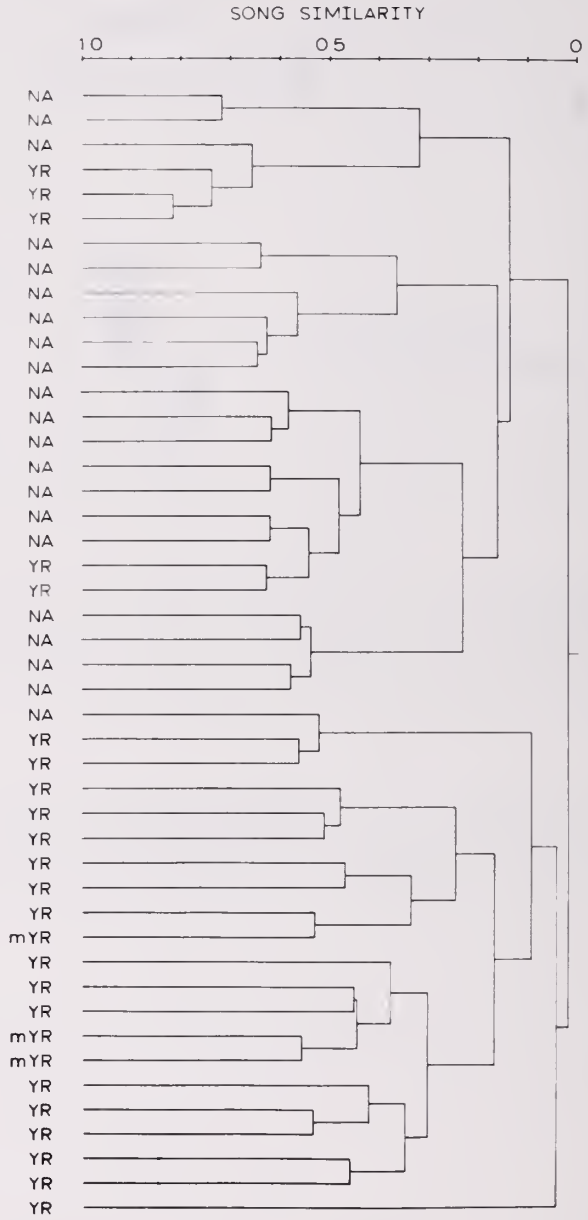

FIG. 3. Dendrogram of song similarity based on element shape. Mimic Yellow-rumped Warbler songs are composed of elements similar to those of typical Yellow-rumped Warblers. NA = Nashville Warbler; YR = typical Yellow-rumped Warbler; mYR = mimic Yellow-rumped Warbler.

are $P < 0.001$, $P < 0.001$, and $P < 0.10$). All five tempo and frequency variables contribute significantly to the discriminant function ($P < 0.0001$, Rao's V); this function produces a highly significant degree of separation of groups (Wilks' Lambda = 0.1107, $P < 0.0001$).

Classification of songs according to element shape gives imperfect distinction between species (Fig. 3). Two major clades are recognizable in the dendrogram of song similarity: the upper group contains 20 of the 21 Nashville Warblers and five Yellow-rumped Warblers; the lower group contains the remaining 21 Yellow-rumped Warblers and one Nashville Warbler. Song elements of mimic Yellow-rumped Warblers do not differ from those of typical Yellow-rumped Warblers by this analysis.

Censuses of breeding birds on all islands indicated that Yellow-rumped Warbler song characteristics were unaffected by the presence of nearby singing Nashville Warblers. There is no relationship between the discriminant scores of Yellow-rumped Warbler songs and the relative abundance of Nashville Warblers (no. Nashville/no. Yellow-rumped) on the islands at which they were recorded ($r_s = 0.231$, N = 25, $P > 0.10$). In addition, at least one mimic Yellow-rumped Warbler bred on an island which contained no Nashville Warblers. These results suggest that Nashville song characteristics were not learned by mimic Yellow-rumped Warblers as the two species established territories together on their breeding islands.

Discussion.—Mimicry of Nashville Warblers occurs infrequently among Isle Royale Yellow-rumped Warblers, and consists of imitation of the general structure of Nashville songs (i.e., tempo and frequency; Fig. 2), but not of the configuration of song elements (Fig. 3). Yellow-rumped Warbler mimicry could result from misdirected song learning early in development. Imitation of Nashville Warblers apparently does not occur among adult Yellow-rumped Warblers, since high Nashville Warbler densities do not produce Nashville characteristics in the songs of nearby Yellow-rumped Warblers. Rather, incorrect song acquisition may result from the exposure of juvenile Yellow-rumped Warblers to Nashville Warbler song during their first summer, when song learning has been shown to occur (Marler and Peters 1977; Baptista and Morton 1981; Slater and Ince, Ibis 124:21–26, 1982). Exposure of juvenile birds to songs of allospecifics may be fairly extensive because both species are common in the study area.

We lack a sufficient understanding of the conditions under which normal song learning may take place. As yet there is no predictive model for assessing the outcome when these conditions are violated, even after 15 years of controlled experiments (Marler, pp. 231–244 *in* Proc. XIV Int. Ornithol. Congr., 1967; Payne, Anim. Behav. 29:688–697, 1981). We are farther from an understanding of abnormal song learning in the field (Kroodsma et al. 1983). Studies such as this one increase our understanding of avian song learning by documenting conditions under which normal song development fails to occur.

A final caveat—this analysis has ignored the multiple song types sung by many parulines, including the Yellow-rumped Warbler (M.R. Lein, pers. comm., cited in Kroodsma, Auk 98:743–751, 1981). Morse (Nature 226:659–661, 1970), Lein (Can. J. Zool. 56:1266–1283, 1978), and Kroodsma (1981) have shown that warblers use different songs in different contexts: the Type I song of Kroodsma (1981) is used in male-female interactions, whereas the Type II song occurs in intrasexual confrontations. A second group of studies has suggested that song repertoires in density limited populations may serve to repel newcomers by creating the false impression that many birds occupy the territory of a single male ("Beau Geste" hypothesis; Krebs, Anim. Behav. 25:475–478, 1977; Krebs et al., Nature 271:539–542, 1978; Yasukawa, Anim. Behav. 29:114–125, 1981; but see Dawson and Jenkins, Behaviour 87:256–269, 1983). An evaluation of the function of mimic songs in the Isle Royale Yellow-rumped Warbler population is not possible without knowing whether the songs were male- or female-directed. However, my observations indicate that mimic Yellow-

rumped Warblers may not sing multiple song types. Two of the four mimic Yellow-rumped Warblers were observed regularly through June and early July; neither bird was heard singing a typical song or an unfamiliar mimic song.

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Misdirected displays by a solitary bird of paradise in an oropendola nesting colony.—On 19 March 1979 we spent the day roaming the forest on Little Tobago Island, a 113-ha hilly islet lying 2 km off the northeast coast of Tobago. Our objective was to track down any surviving remnants of a colony of about 50 Greater Birds of Paradise (*Paradisaea apoda*) transported from the Aru Islands off New Guinea as a conservation measure by W. Ingram in 1909 and 1912 (Ingram, Avic. Mag. 18:142–147, 1911; 23:341–351, 1917). Roldan George, the government-employed conservator for the islet and its seabird colonies thought that one male and possibly one female remained, and steered us to the south end of the island where he felt the male might be found. Here, in two tall palm trees (*Roystonea oleracea*) emerging above the 15-m canopy of deciduous trees a dozen or more Crested Oropendolas (*Psarocolius decumanus*) were singing and displaying noisily, among their long, pendulent nests. In the midst of the group was a single adult male bird of paradise, in full display. This bird was clearly a member of the displaying group, and we watched for an hour through the screening canopy as the bird displayed, repeatedly throwing its body and wings forward with plumes fanned upwards in typical *P. apoda* display patterns (Wallace, The Malay Archipelago, Harper, New York, New York, 1869; Gilliard, Natl. Geogr. Mag. 114:428–440, 1958; Dinsmore, Auk 87:305–321, 1970). Dominance and territorial relationships were difficult to determine, but the bird of paradise clearly maintained a central position in the colony and was rarely, if ever, displaced during an hour of almost continuous displaying.

Ingram's colony, despite evidence of successful breeding in early decades, has declined continuously with one or more catastrophic drops (Dinsmore, Carib. J. Sci. 10:93–100, 1970). Baker (Bird-Lore 25:295–302, 1923) observed 15 or 16 birds in one tree in the early 1920's, but other observers in that period were less successful. On a 3-week visit in 1958, Gilliard (1958) recognized 15 different individuals and estimated that as many as 35 birds might still be present. However, a hurricane in 1963 destroyed much of the forest habitat on the island and no more than nine birds have been counted since that time. Dinsmore (1970), in his intensive 9-month study of the birds in 1965–66, found only seven birds: four males and three female-plumaged (female or juvenile) birds. Four males and one female were still present in 1968 (Dinsmore 1970) but records since 1970 have been limited to an occasional sighting of a single bird (R. George, pers. comm. to Dinsmore). Residents of Speyside, a coastal town directly opposite the islet, continue to propagate rumors of one or two birds, but Richard ffrench of Pointe-a-Pierre, Trinidad, an active ornithologist who contacts many of the ornithological visitors to the area, has been unable to confirm these

rumors in recent years. Ralph Morris (pers. comm.) saw none during an extended study of the seabirds of Little Tobago in 1975–76, but, to his surprise, encountered a single male in full display on 25 February 1981, close to the spot where we made our observations in 1979.

Single birds reared in isolation from conspecifics often form strong and persistent social bonds with their surrogate associates, using them as targets for species-characteristic displays in contexts of flocking, mating, and sexual activity. We can only guess what the post-fledging social environment of our displaying bird may have been, but with the colony in its terminal phase, possibly reduced to a single bird, opportunities for conspecific interactions must have been limited at best. We therefore speculate that the displaying oropendolas filled a gap in the social umwelt of this individual, providing releasers for its innately programmed and motivated display movements. Superficially the Crested Oropendola is remarkably similar to the Greater Bird of Paradise in size, general coloration (rich browns and golden yellows predominating), vocalizations (raucous screeches and nasal calls), and even display movements (deep bows, spread wings, and forward tumbles). Birds of paradise, furthermore, are noted for a high frequency of misdirected displays and of hybridization in the wild and in zoos (Diamond, pers. comm.).

Oropendolas have been and remain abundant on Little Tobago, especially in the deciduous forest stands favored by the birds of paradise. Birds of paradise generally ignored and numerically dominant oropendolas on the islet (Dinsmore, M.S. thesis, Univ. Wisconsin, Madison, Wisconsin, 1967), but a single individual that strayed to Tobago in the early days of the colony was found associating with a flock of oropendolas (Baker 1923). Although birds of paradise dominated with mild but effective threat displays in all of four direct, between-species encounters observed by Dinsmore (1967), he speculated that behavioral interactions with oropendolas might become detrimental to the former as they, normally a lek species, decreased in numbers. ffrench (pers. comm.) at one point suggested that oropendolas with their numerical dominance and similar displays might adversely affect the ability of birds of paradise to attract mates of their own species.

Acknowledgments.—We are grateful for information and suggestions to J. Davies, J. Dinsmore, R. ffrench, R. George, R. Morris, and B. Worth.—John T. Emlen and Virginia M. Emlen, *Dept. Zoology, Univ. Wisconsin, Madison, Wisconsin 53706.* *Accepted 7 Mar. 1984.*

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Nest spacing, colony location, and breeding success in Herring Gulls.—In large-bodied, colonial-nesting *Larus* gulls, conspecific predation of eggs and chicks by neighbors represents a potential reproductive cost (Parsons, J. Anim. Ecol. 44:553–573, 1975). Egg and chick loss to neighbors can be substantial (Brown, Ibis 109:502–515, 1967; Parsons, Br. Birds 64: 528–537, 1971), and such predation is particularly severe in high nest density areas (Hunt and Hunt, Ecology 57:62–75, 1976; Butler and Trivelpiece, Auk 98:99–107, 1981).

There are two principal differences between adjacent Herring Gull (*Larus argentatus*) colonies near Port Colborne, Niagara Co., Ontario, Canada. One colony (Canada Furnace) is on the mainland and nests are distributed over an area of about 4 ha. A nearby (0.6 km to the west) colony (Lighthouse) is insular and nests are concentrated on an elevated rock pile about 0.5 ha (see Morris and Haymes, Can. J. Zool. 55:796–805, 1977 for further details of the locations). Similar numbers of birds nest at each site (80–100 pairs in recent years) in association with Ring-billed Gulls (*L. delawarensis*). In 1981 we quantified the different

nest dispersion patterns at the two sites. We also obtained hatching and chick survival data for Herring Gull pairs that laid three-egg clutches during the egg-laying 'peak' at both locations. Our objective was to assess the probable influences of: (1) nest spacing pattern, and (2) colony location on these reproductive parameters.

Methods.—We used identical procedures at both colonies. Each location was visited daily from mid-April until early June 1981 and every 3 days thereafter. Eggs were marked when first found and their length and breadth measured to the nearest 0.1 mm with vernier calipers. The temporal distribution of clutch initiation was determined for all pairs at both locations.

Hatching and chick survival data were obtained for 23 pairs at Canada Furnace and 30 pairs at the Lighthouse. Each pair laid three-egg clutches during a 'peak' period of egg-laying in late April (see below). At Canada Furnace, most pairs (N = 16) were on a boulder-covered shelf adjacent to Lake Erie or on a ridge next to a small, inland pond; the remainder (N = 7) were on elevated knolls within a Ring-billed Gull colony. At the Lighthouse, each pair was within a 15-m radius of an observation blind. Nest checks for these pairs were carried out during the incubation and early brooding periods by walking to all nests. At the Lighthouse, a second observer was in the blind during nest checks and both observers remained in the blind for about 1 h after each visit. The purpose was to note the behavior of adults during and following our presence in the colony. Egg fates, hatching success, and chick losses were recorded during these visits until chicks in study nests were mobile. Thereafter, chick fates were determined from the blind (Lighthouse) or a portable platform (Canada Furnace) with the use of a spotting telescope. When chicks were not seen during two consecutive observation periods, a nest check was made to determine the fate of missing chicks. Chick fates were followed until the youngest chick within a brood was 21 days old.

Internest distances of all Herring Gull pairs were measured at each colony in early August to avoid disturbance during the breeding season. At Canada Furnace, internest distances were measured in the field for nests less than 15 m apart. More widely spaced nests were plotted onto a scaled aerial photograph of the site and internest distances determined from the photograph. At the Lighthouse, internest distances of all nests were measured in the field.

Results.—Ring-billed Gulls nested in association with Herring Gulls at both locations. At Canada Furnace, most of the 96 Herring Gull pairs were around the periphery of the Ring-billed Gull colony; the remainder were on elevated knolls within it. At the Lighthouse, all 87 Herring Gull pairs nested on an elevated rock pile immediately adjacent to the Ring-billed Gull colony. All Herring Gulls at both sites had another Herring Gull pair as their nearest neighbor.

Nest dispersion patterns.—A nearest-neighbor analysis (Clark and Evans, Ecology 35:445–453, 1954) showed that Herring Gull nests at Canada Furnace (N = 96) were aggregated (R = 0.776) while those at the Lighthouse (N = 87) were evenly distributed (R = 1.26). Each pattern was significantly different from random (statistic C = [CF] = 4.21, C [LH] = 4.5, $P < 0.003$) and each was different from the other (ANOVA, $F = 46.77$, $P < 0.05$). Lighthouse pairs nested significantly closer to one another than Canada Furnace pairs (Mann-Whitney *U*-test, $z = 19.45$, $P < 0.0003$). The mean internest distance ($\bar{r}_A$) at Canada Furnace (12.11 m) was more than three times that at the Lighthouse (3.76 m).

Timing of clutch initiation.—The mean date of clutch initiation at Canada Furnace (28 April 1981, SD = ±7 days) was not significantly different from that at the Lighthouse (30 April 1981, SD = 6.5 days; *t*-test, $P > 0.1$). While new clutches were laid through the end of May at both locations, more than half of the total number of clutches at each site (CF = 52%, LH = 56%) were initiated during a 9-day period of 22–30 April (Canada Furnace) and 27 April–5 May (Lighthouse). These dates were taken as the egg-laying 'peak' at each colony.

TABLE 1

THE FATES OF HERRING GULL CHICKS THAT DIED OR DISAPPEARED BEFORE 21 DAYS OF AGE[a]

Colony site	Chicks lost (N)			
	Dead			
	Near own nest[b]	Near another nest	Disappeared	Total
Canada furnace	3 (11%)	9 (32%)	16[c] (57%)	28
Lighthouse	13[d] (68%)	2 (11%)	4[d] (21%)	19

[a] Fifty-nine chicks hatched from 22, three-egg clutches at Canada furnace and 66 chicks hatched from 30, three-egg clutches at the lighthouse.
[b] Within 1.5 m of nest cup.
[c] 14 older than 4 days of age.
[d] All younger than 4 days of age.

The data which follow are based on the three-egg clutches noted earlier (CF = 23 pairs, LH = 30 pairs) that contained first eggs during the peak periods of egg-laying at each colony.

Egg volume.—Within-clutch comparisons of egg volume ($V = LB^2 0.476$) for the 23, three-egg clutches at Canada Furnace (1st vs 3rd egg, $t = 2.44$, $P < 0.05$; 2nd vs 3rd egg, $t = 2.75$, $P < 0.05$) and the 30, three-egg clutches at the Lighthouse (1st vs 3rd egg, $t = 3.79$, $P < 0.05$; 2nd vs 3rd egg, $t = 4.50$, $P < 0.05$) showed that first and second eggs were significantly larger than third eggs. Comparisons of the volumes of first, second, and third eggs from clutches at Canada Furnace against their counterparts at the Lighthouse showed no differences (Mann-Whitney *U*-tests, $P > 0.2$).

Hatching and chick survival.—One of the 23 clutches at Canada Furnace was destroyed by a rock slide. Hatching success of the remaining 22, three-egg clutches at Canada Furnace was marginally higher than that of the 30, three-egg clutches at the Lighthouse (number of clutches hatching 3, 2, 1 or 0 eggs, 1 and 0 eggs pooled, $\chi^2 = 5.44$, df = 2, $0.1 > P > 0.05$). The primary factor contributing to egg failure at both colonies was addled eggs (CF, N = 4, 57%; LH, N = 15, 63%). The factor of second importance at Canada Furnace was eggs that "died" while pipping (N = 2, 29%) whereas, at the Lighthouse, it was eggs that disappeared before hatching (N = 4, 17%). No eggs disappeared at Canada Furnace.

Chick survival (to at least 21 days of age; Dexheimer and Southern, Wilson Bull. 86:288–290, 1974) at the Lighthouse (1.57 ± 0.97 chicks per pair) was significantly higher than that at Canada Furnace (1.41 ± 1.08 chicks per pair; Mann-Whitney *U*-test, $z = -2.19$, $P = 0.014$). The fates of chicks that failed to reach 21 days of age are shown according to known death or disappearance (Table 1). The distribution of losses due to these factors was significantly different at the two colonies ($\chi^2 = 6.1$, df = 1, $P < 0.02$). Of chicks found dead at Canada Furnace, the majority (N = 9, 75%) were near nests other than their own. At the Lighthouse, the majority (N = 13, 87%) were found near their own nests. The difference in location of dead chicks was significant (Fisher test, $P = 0.002$). Most chicks that disappeared at Canada Furnace (N = 14) were older than 4 days of age; all those that disappeared at the Lighthouse (N = 4) were younger than 4 days of age.

Chick survivorship.—Survivorship curves for chicks at the two sites are in Fig. 1. Chick losses at Canada Furnace occurred at a nearly constant rate over the 21 days after hatching, whereas at the Lighthouse, losses were highest in the 4 days following hatching. At Canada Furnace, eight (29%) chicks died or disappeared in the first 4 days after hatching; at

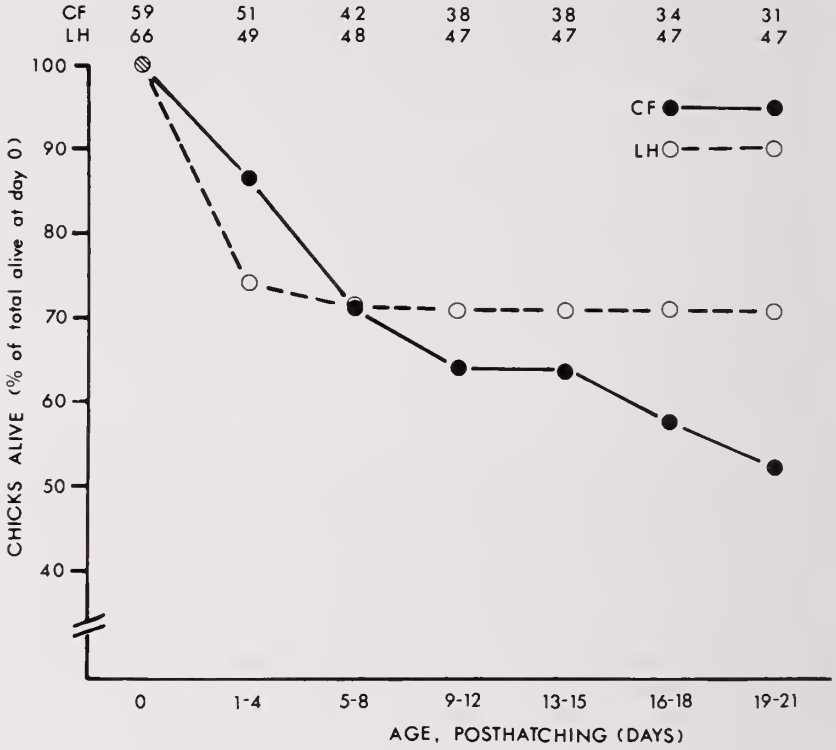

FIG. 1. Herring Gull chick survival through 21 days after hatching, for 22, three-egg clutches at Canada Furnace (CF) and 30, three-egg clutches at the Lighthouse (LH). The number of chicks alive at the start of each age class is shown at the top of the figure.

the Lighthouse, 17 (89%) chicks were lost during the same period. The rates of loss with respect to chick age (days) were different at the two sites (CF, linear regression, df = 6, r = 0.96, $P < 0.05$; Lighthouse, negative exponential, df = 6, $r = 0.71$, $P < 0.05$).

Discussion.—Differential breeding success of pairs within a larid colony can be explained by asynchrony in the seasonal timing of egg-laying (Coulson and White, Proc. Zool. Soc. London 136:207–217, 1961; Chardine and Morris, Ibis 125:389–396, 1983), clutch-size differences when clutches are initiated at the same time (Harris, Ibis 106:432–456, 1964; Brown 1967; Parsons 1975), age of parents (Davis, Ibis 117:460–473, 1975; Ryder, Wilson Bull. 87:534–542, 1975; Mills, Ibis 121:63–67, 1979), and nest location within a colony (Haymes and Blokpoel, Wilson Bull. 92:221–228, 1980; Pugesek, Behav. Ecol. Sociobiol. 13:161–171, 1983). In our between-colony study, we attempted to control for these confounding variables by restricting the comparison to selected pairs at each location. The pairs chosen were similar in their clutch-size, egg volume, and timing of clutch initiation.

Although numbers were small, more eggs disappeared at the Lighthouse than at Canada Furnace, a trend consistent with an earlier study (Morris and Haymes 1977). In 1981 more chicks were lost at Canada Furnace than at the Lighthouse. There were major differences

between the two colonies both in the age of chicks that disappeared, and in the age and location of dead chicks. At Canada Furnace, chick losses occurred at a constant rate over the 21-day post-hatch period, whereas, at the lighthouse, most chicks died or disappeared within 4 days of hatching.

Two factors likely contributed to these differences. First, Canada Furnace was on the mainland and people and dogs regularly trespassed through the site, often many times during a day (J. Bonisteele, pers. comm.). During these disturbances (several in our presence), mobile chicks scattered widely from their home nests and were attacked by other Herring Gull parents as they attempted to return. The constant loss of chicks from hatching to 21 days of age, and the greater number of dead chicks found away from their nest-sites, were likely related to these frequent disturbances. Conversely, at the Lighthouse, human disturbance was infrequent as the site is accessible only by boat. Furthermore, potential human intruders were hesitant to enter the colony as communal "mobbing" is common there. From our observations, this was not the case among the more widely dispersed pairs at Canada Furnace (cf. Anderson and Wiklund, Anim. Behav. 26:1207–1212, 1978).

Second, egg disappearance, chick disappearance prior to 4 days of age, and the large number of young chicks found dead near their own nests at the Lighthouse, implicate neighboring Herring Gull adults as the causative factor. Herring Gulls are known cannibals (Parsons 1971) and both cannibalism and attacks by neighbors are more likely to occur when nests are close together (Brown 1967; Hunt and Hunt, Auk 92:270–279, 1975). We suggest therefore that neighboring Herring Gulls were the primary factor contributing to both the death and disappearance of young chicks at the Lighthouse.

There are at least two alternative explanations for the differences in egg loss and chick survival patterns observed at the two colonies. These are: (1) differences in food availability, and (2) differences caused by investigator disturbance. Hungry chicks are particularly susceptible to attacks by neighbors (Hunt and McLoon, Auk 92:523–527, 1975). Although we have no data on food availability, shortages would be expected to have a similar impact on chicks at the two colonies as they are very close together and adults from them foraged in the same areas (see Morris and Black, J. Field Ornith. 51:110–118, 1980; Morris, unpubl.).

Investigator disturbance in seabird colonies has been implicated as a factor reducing both egg and chick survival (Robert and Ralph, Condor 77:495–499, 1975; Fetterolf, Wilson Bull. 95:23–41, 1983). We recognized this factor as a potential problem and chose pairs for the comparison (from those available as peak nesters) based on ease of investigator access. At Canada Furnace, nests were selected for visibility from a distance such that chick counts could be made with a spotting telescope. Closer approach to a particular nest was made infrequently and only when an obvious chick loss had occurred. At such times, chicks crouched in available rock cover adjacent to their nests. At the Lighthouse, pairs selected were all close to the observation blind and nest checks were usually unnecessary as dead chicks could be readily seen without leaving the blind. These procedures were designed to equalize negative effects of investigator disturbance. Our observations from the blind during and following nest checks at the Lighthouse, showed that mobile chicks also remained in the immediate vicinity of their nests, crouched among available rock cover. Adults at both locations always settled down and exhibited normal incubation and chick feeding behavior within minutes of our departure (cf. Chardine and Morris, Wilson Bull. 95:477–478, 1983). We think it unlikely, therefore, that the differences observed, particularly in chick survival data, can be explained either by differences in food availability or by differences in our activities within the colonies.

In Western Gulls (*L. occidentalis*), pairs whose chicks were killed by neighbors nested closer together than pairs that had no chicks killed (Hunt and Hunt 1975). In Glaucous-winged Gulls (*L. glaucescens*), high chick mortality due to conspecific aggression was most

common shortly after hatching and more frequent on small breeding territories than on larger ones (Hunt and Hunt 1976). In our study, the high incidence of young, dead chicks near their own nest at the Lighthouse suggests a higher risk there due to neighbor proximity. This is consistent with the observation that gulls nesting at high density fledge (on average) fewer chicks than pairs in low density areas (Butler and Trivelpiece 1981). However, while neighbor-interference was less frequent among the lower density Canada Furnace pairs, the pairs there apparently suffered excessive loss of mobile chicks because of easy access by humans and dogs to the mainland nesting location.

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Nest-site selection and breeding biology of the Chipping Sparrow.—Despite its extensive breeding range (Godfrey, The Birds of Canada, Natl. Mus. Can. Bull. 203, 1966) and frequent habit of nesting in man-made clearings, few studies of the breeding biology of the Chipping Sparrow (*Spizella passerina*) have been published. This study examines several aspects of Chipping Sparrow biology (e.g., chronology of the nesting cycle, breeding success, and nestling growth), and emphasizes relationships between nesting success and components of nest-site selection, such as nest height and orientation.

Study site and methods.—The study was done from 25 May–15 July 1981 and 25 May–8 July 1982 in Algonquin Provincial Park, Nipissing District, Ontario. Algonquin Park lies on the southern edge of the Canadian Shield in a transition zone between conifers typical of more northerly regions and southern hardwoods. White spruce (*Picea glauca*), white pine (*Pinus strobus*), and balsam fir (*Abies balsamea*) are dominants in the study area (see Maycock, Ecology 37:846–848, 1956, for a complete description of the local vegetation).

We located nests by observing adults during nest construction and by searching in suitable habitats. Nests were visited daily between 17:00 and 20:00. In 1981, nestlings were marked on their tarsi with a felt pen for individual identification, and each day we measured nestling weight, tarsus length (from tibiotarsus-tarsometatarsus joint to hallux), bill length (from anterior edge of nares to tip of culmen), and bill width (at anterior edge of nares). Adult measurements were based upon 30 specimens from Ontario in the collection of the Royal Ontario Museum (no difference between the sexes).

After the young had fledged, the heights of the nest and nest tree were measured or estimated, and orientation of each nest (i.e., the side of the tree in which it was built), was recorded. The nest was then collected and its composition analyzed.

For each nest, the percentage cover of each plant species within 1 m of the nest (including nest tree) was estimated. Nearby trees were characterized by the point-quarter method (Smith, Ecology and Field Biology, 3rd ed., Harper and Row, New York, New York, 1980). Within each quadrant, the distance from the nest to the nearest tree over 1 m tall was measured, the tree identified, and its height measured or estimated. (The nest tree was not included in the analysis.) A minimum height of 1 m was used because this was the lower

TABLE 1
VEGETATION AT CHIPPING SPARROW NEST-SITES

Tree species nearest to nests[a]	No. quadrants[b]	% frequency
White spruce (*Picea glauca*)	38	45
Trembling aspen (*Populus tremuloides*)	9	11
Balsam fir (*Abies balsamea*)	7	8
White pine (*Pinus strobus*)	7	8
Choke cherry (*Prunus virginiana*)	7	8
Red pine (*Pinus resinosa*)	4	5
Red maple (*Acer rubrum*)	2	2
Sugar maple (*Acer saccharum*)	2	2
Total	76	89
Plant species with the highest mean percent covers within 1 m of nests[c]	**Mean % cover**	**% frequency**
White spruce	39	91
Grass species (mostly *Danthonia spicata*)	20	82
Hairy-cap moss (*Polytrichum* sp.)	9	45
Blueberry (*Vaccinium angustifolium*)	6	45
Red pine	6	6
Balsam fir	5	14

[a] The following occurred in one quadrant only: *Alnus rugosa*, *Amelanchier* sp., *Betula papyrifera*, *Corylus cornuta*, *Pinus banksiana*, *Salix* sp., *Sambucus pubens*, and unidentified dead. In four quadrants there were no trees within 100 m of the nests.

[b] Four quadrants/nest.

[c] Mean percent of bare ground was 5%, and its percent frequency was 23%.

limit to heights of nest trees in this study, i.e., trees taller than 1 m were considered potentially suitable for nesting.

Nestling growth rates are described quantitatively using the method of Ricklefs (Ecology 48:978–983, 1967). All means are given ±1 standard deviation (SD). Statistical significance was set at $P < 0.05$.

Arrival on breeding grounds, pair formation, and nest initiation.—The first Chipping Sparrows were noted in Algonquin Park during the last week of April each year (pers. obs.; R. G. Tozer, pers. comm.). Most of the population arrived during the first week of May, at which time males were seen singing from conspicuous perches, usually in white spruce or balsam fir.

Territorial disputes occurred frequently in mid-May but declined progressively thereafter. Disputes included chases during which resident males sang short phrases in flight as they closely pursued conspecific intruders. By late May most adults were paired and spent considerable time foraging on the ground along the edges of wooded areas, gravel roads, and parking lots.

We observed 15 copulations, all of which occurred on tree branches. In contrast, Walkinshaw (Wilson Bull. 56:193–205, 1944a) reported that copulation generally occurred on the ground. On two occasions copulation immediately followed territorial disputes, with the resident male returning to his mate after chasing away an intruder.

The modal date of nest initiation, calculated by direct observations or back-dating, was

TABLE 2
CLUTCH-SIZES AND NESTING SUCCESS OF CHIPPING SPARROWS

	1981	1982	Combined	*P*
Clutch-size $\bar{x}$	3.8	4.3	4.0	NS[a]
SD	0.6	0.5	0.6	
N	10	7	17	
range	3–5	4–5	3–5	
% eggs hatched[b]	65.4 (36/55)	80 (24/30)	70.6 (60/85)	NS[c]
% nests hatching ≥1 young	66.7 (10/15)	85.7 (6/7)	72.7 (16/22)	NS[c]
% young fledged of those hatched	72.2 (26/36)	100 (24/24)	83.3 (50/60)	<0.005[c]
% nests fledging ≥1 young	53.3 (8/15)	85.7 (6/7)	63.6 (14/22)	NS[c]

[a] Mann-Whitney *U*-test.
[b] Losses due to predation.
[c] *G*-test.

31 May. This date calculation includes our data and an additional 15 Chipping Sparrow nests from Algonquin Park (Ontario Nests Records Scheme). A few nests which were started through early July presumably were replacement clutches; we have no evidence of double-brooding.

Nest-site selection.—Nineteen of the 22 nests (86.4%) were placed in white spruce, and one each was in eastern hemlock (*Tsuga canadensis*), balsam fir, and red pine (*Pinus resinosa*). Although white spruce also predominated in the sample of tree species nearest the nest tree (Table 1), its frequency of occurrence was only 45.2%. The difference between frequency of occurrence of white spruce and its use as a nesting substrate by Chipping Sparrows was significant ($G = 12.49$, 1 df, $P < 0.001$). The analysis assumes that the trees around nests are a random sample of trees in the immediate area. Thus, the birds selected white spruce as the nest tree, rather than nesting in species of trees according to their relative abundance in the immediate habitat.

The median height of nest trees was 2.5 m (range = 1.1–13.7 m). This height did not differ significantly from nearby trees (Mann-Whitney *U*).

The most common trees in the vicinity of nests and the dominant plants within 1 m of nests (Table 1) are typical early secondary successional species in well-drained areas in Algonquin Park. These species are characteristic in areas which have been disturbed by fire (Martin, Ecol. Monogr. 29:187–218, 1959), as well as by man. This supports the idea that the dramatic increase in edge habitats and open areas associated with European man's arrival in North America may have permitted Chipping Sparrows to greatly increase in numbers (Stull, U.S. Natl. Mus. Bull. 237, Pt. 2, 1968:116).

The mean height of nests was 1.1 ± 0.6 m (range = 0.4–2.5 m), which generally agrees with findings of others (e.g., Stull 1968; Tate, Diss. Abstr. Int. 34B:1982–B, 1973; Buech, J. Field Orn. 53:363–369, 1982).

Nest characteristics.—Nest construction required 4 days. Although we did not make detailed observations on division of labor, both sexes in each of two pairs were seen gathering material and incorporating it into their nests. In contrast, Stull (1968) and Walkinshaw (1944a; Bird-Banding 23:101–108, 1952), reported that only females built nests. Furthermore, in other species of *Spizella*, only females have been observed building the nest (e.g.,

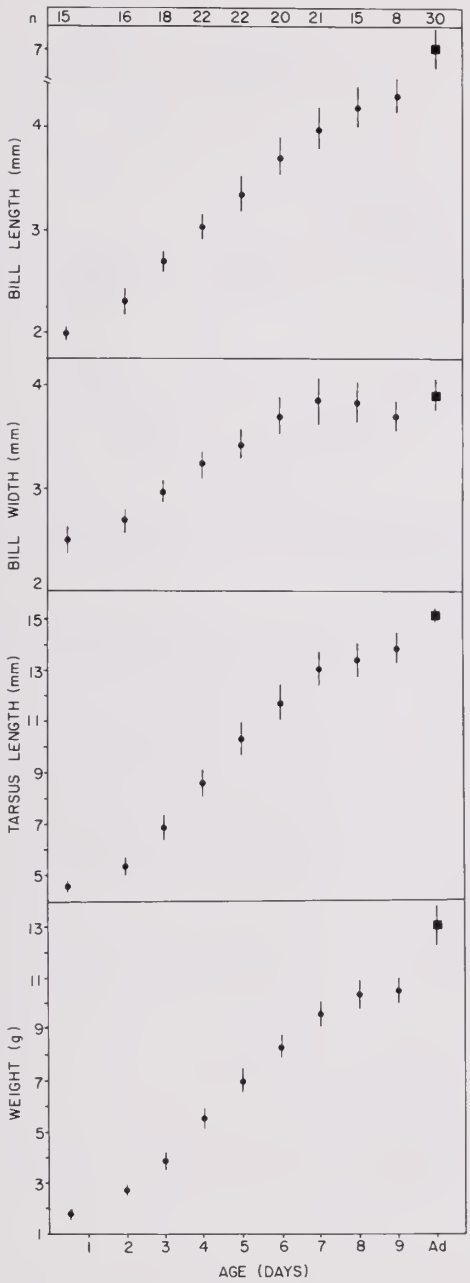

FIG. 1. Growth of nestling Chipping Sparrows. Means are given ±1 SD; sample sizes are given across the top of the figure. Measurements of 30 adults (Ad) are included for comparison.

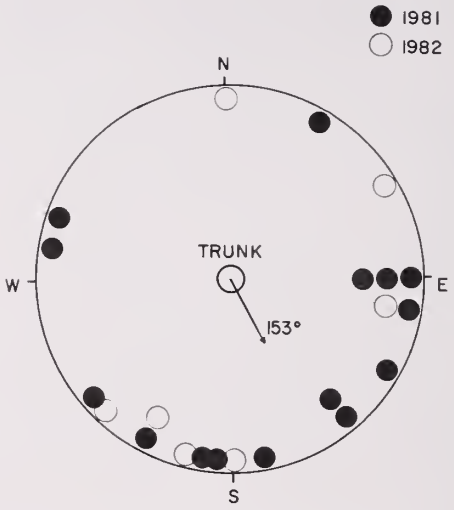

FIG. 2. Orientations of Chipping Sparrow nests around the nest trees. The central vector shows the mean orientation.

Clay-colored Sparrow [*S. pallida*]; Walkinshaw, Jack-Pine Warbler 22:120–131, 1944b). The extent of the male Chipping Sparrow's contribution to nest-building requires further clarification.

The outer cups of nests were composed of stems of grasses and other plants, and small roots. Nests were generally lined with fine roots and small amounts of animal hair. Four nests were lined almost exclusively with bright, golden-colored sporophyte stalks of moss (*Polytrichum* sp.).

Clutches.—The first egg was laid the day after nest construction was finished, and one egg was laid daily until the clutch was completed (see also Walkinshaw 1944a, 1952). The mean clutch-size was 4.0 ± 0.6. Clutch-sizes in 1981 and 1982 were not significantly different (Mann-Whitney *U*; Table 2).

The incubation period, defined as the interval from laying the last egg to hatching of the last young, was 11–12 days, a value consistent with the findings of Dawson and Evans (Physiol. Zool. 30:315–327, 1957), and Walkinshaw (1944a). In some nests, all eggs hatched within a few hours of each other; in others, hatching was spread over 24 h. Asynchronous hatching also was noted by Walkinshaw (1944a).

Nestling growth.—At hatch nestlings weighed 1.2–1.4 g. Nestling weight, tarsus length, and bill length and width grew in sigmoid fashion (Fig. 1), a pattern typical of most avian species (Ricklefs, Ibis 110:419–451, 1968).

The value of the growth curve index, k (Ricklefs 1967), for weight gain was 0.542. This value closely resembles the rate constants calculated by Ricklefs (1968), who reported k = 0.536 for Weaver's (Auk 54:103–104, 1937) New York study, 0.552 for Walkinshaw's (1944a) Michigan study, and 0.544 for Dawson and Evans' (1957) Michigan study. Relative to other avian species (c.f. Ricklefs 1968), there appears to be little geographic variation in the growth rate of Chipping Sparrows in northeastern North America.

Most young fledged at 9 days (±1 day) of age. Weight, tarsus length, and bill width of

fledglings can be compared with adult measurements in Fig. 1. Human disturbance of the nestlings may lead to premature fledging (Walkinshaw 1944a, Dawson and Evans 1957, Stull 1968). However, the various body dimensions reported were all asymptotic by day 8 or 9, so although the natural fledging age may be a day or two later, these measurements still represent true fledgling size.

Nest orientation and nest success.—In Algonquin Park, 77% (17 of 22) of nests were situated on the south or east sides of the trees (Fig. 2). The average orientation was 153.3° with an angular deviation of s = 63.7° (Batschelet, Circular Statistics in Biology, Academic Press, New York, New York, 1981). This degree of concentration was statistically significant ($r = 0.382$, Rayleigh test), and there was no significant difference in mean orientation between years (Mardia-Watson-Wheeler test, Batschelet 1981). There were no directional biases with respect to distances from nests to nearest trees (mean distance = 1.9 ± 1.6 m, N = 22, Mann-Whitney *U*).

Nest success for 1981 and 1982 is summarized in Table 2. In general, there was a trend toward lower success rates in 1981 than 1982. In 1982 all nestlings fledged (N = 24), whereas in 1981, 72% (26 of 36) fledged ($P < 0.005$, df = 1, *G*-test). In 1981 there was a relationship between nest height and success. Successful nests averaged 1.51 ± 0.64 m in height (range = 0.64–2.46, N = 8). Unsuccessful nests averaged 0.69 ± 0.29 m (range = 0.38–1.30, N = 7). The difference was significant ($P = 0.01$, Mann-Whitney *U*-test), and suggests a relationship between nest height and success in 1981 which, however, did not exist in 1982.

Successful nests averaged 158.1 ± 48.6° (N = 14), which is only 4.8° from the overall mean. Unsuccessful nests averaged 28.7 ± 76.3° (N = 8), or 124.6° from the overall mean. The difference was statistically significant ($P < 0.05$, Rank-sum test, Batschelet 1981).

Biases in nest orientation have generally been interpreted in terms of amelioration of the microenvironment (e.g., Cactus Wrens [*Campylorhynchus brunneicapillus*], Austin, Condor 76:216–217, 1974; Abert's Towhees [*Pipilo aberti*], Finch, Condor 85:111–113, 1983). However, all nest failures in the present study were attributable to predation (inferred from disappearances of clutches of eggs or nestlings). No instances of nest parasitism by Brown-headed Cowbirds (*Moluthrus ater*) were recorded, in contrast to Buech (1982). Nests on the southeast sides of trees were not better concealed from us, but because we lack information on the kinds of predators and their hunting methods, extrapolations would be hazardous.

Ultimately, thermoregulation of nestlings may be facilitated by southeastern orientation. Most nests were situated such that they were largely exposed to the early morning sun. Also, because the prevailing winds in the Algonquin Park area are from the northwest (Environment Canada, Canadian Normals, Vol. 3, Wind, 1975), the birds may gain some degree of protection from wind and rain by placing their nests on the opposite side of trees. The relative importance of predator avoidance and climatic moderation in nest-site selection requires further study.

Acknowledgments.—We thank J. C. Barlow for allowing us access to bird specimens and nest records of the Ontario Nest Records Scheme at the Royal Ontario Museum. He also provided helpful comments on an earlier draft of the manuscript, as did F. Cooke, J. C. Davies, C. L. Gratto, J. Hamann, K. Martin, H. McBrien, and G. Ménard. Critical comments by L. B. Best and T. Rich are also appreciated.—JOHN D. REYNOLDS, *Dept. Biology, Queen's Univ., Kingston, Ontario K7L 3N6, Canada;* AND RICHARD W. KNAPTON, *Dept. Biological Sciences, Brock Univ., St. Catharines, Ontario L2S 3A1, Canada.* *Accepted 10 Apr. 1984.*

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Comparisons between single-parent and normal Mourning Dove nestings during the post-fledging period.—Reports on the success of single parent Mourning Dove (*Zenaida macroura*) nests observed in the field (Laub, M. S. thesis, Ohio State Univ., Columbus, Ohio, 1956; Haas, Proc. S.E. Assoc. Fish and Wildl. Agencies 34:426–429, 1980) and in captivity (Goforth, Auk 81:233, 1964) have been published previously. The field studies indicated that two squabs could be raised to fledging by a single parent if the squabs were 5–8 days old when the other parent was lost. However, for single-parent nest success to equal normal nest success squabs had to be 9–10 days old when deprived of one parent (Haas 1980). The sex of the parent removed in that study did not influence fledging success. Goforth (1964) reported that a single captive male parent successfully incubated (starting 4 days postlaying) a normal clutch of two eggs and then raised the two squabs until they fledged. However, no studies have reported interactions between single parents and their offspring during the postfledging (PF) interval. Herein we describe such interactions between single female parents and fledgling Mourning Doves.

Behavioral interactions among adult Mourning Doves, 35 radio-tagged nestling/fledglings (12–30 days old), and the single wing-tagged nestmates of 34 of these, were observed during a 2-year study in east-central Alabama (Hitchcock and Mirarchi, J. Wildl. Manage. 48:99–108, 1984). Nestling/fledglings were observed three times daily, from 15 min before to 2 h after sunrise, 12:00–14:00, and 2 h before to 15 min after sunset. Data from two single-parent nests were compared to those from 33 normal two-parent nests. The male parent disappeared between 12 and 15 days posthatching (PH) at one single-parent nest, and before 12 days PH at the other. The following variables were compared: relative number of parental feedings (RNPF = the total number of nestling/fledgling feedings by, or feeding associations with, parents at each age divided by the total length of observation period at each age); net duration of parental feedings (NDPF = length of time nestlings/fledglings were fed at each age divided by number of times nestlings/fledglings were fed at each age); relative duration of fledgling self-feeding (RDFSF = the total time nestlings/fledglings were observed feeding themselves at each age divided by the length of time nestlings/fledglings were actually observed at each age); and relative duration of parental brooding (RDPB = the total time nestlings/fledglings were brooded by parents at each age divided by the length of time nestlings/fledglings were actually observed at each age). The Wilcoxon 2-sample rank sum test was used to examine the significance of any differences between treatment means ($\bar{x} \pm$ SE [N]) because of the lack of normal distributions.

Treatment values for RNPF (N/min) and NDPF (min/N) were summed across selected nestling/fledgling age classes (12, 15–21 days PH) because parent-nestling/fledgling feeding interactions were most critical at that time. Single female parents fed fledglings less often (RNPF, 0.9 ± 0.1 [84], $P = 0.02$) and for shorter periods of time (NDPF, 0.7 ± 0.1 [62], $P = 0.03$) than did those parents still mated (1.2 ± 0.2 [606] and 1.0 ± 0.03 [398], respectively). Although parental feeding rates were reduced, no obvious morphological or behavioral anomalies were detected in the fledglings by the end of the critical dependency period (20–21 days PH). Parent-fledgling feeding interactions normally end at 16 days PH for female parents and between 27 and 30 days PH for male parents (Hitchcock and Mirarchi 1984). In the present study, one single female parent was observed feeding fledglings through 27 days PH and the other through 31 days PH. This extension of parental care probably reflected a reduction in the female's hormonal progression during the reproductive cycle caused by the absence of a mate and/or the time required for establishing a new pair bond and subsequent nest initiation.

Treatment values for RDFSF (min) were summed across 17–21 days PH, and across 24

and 27 days PH because the development of self-feeding techniques and the transition to independence from parental care occurs during these two periods, respectively. There were no differences ($P = 0.78$) in RDFSF between fledglings (17–21 days old) from one and two parent nests (5.3 ± 1.9 [53] and 5.3 ± 0.9 [343], respectively). Consequently, no slowdown in the development of self-feeding behavior was indicated for fledglings from single-parent nests. There also were no differences ($P = 0.74$) in RDFSF between one and two parent nests (20.2 ± 10.2 [10] and 19.0 ± 3.0 [90], respectively) for fledglings 24–27 days old. Apparently the feeding rates of the single female parents were not reduced sufficiently to cause fledglings to increase independent feeding behavior during the transition period from parental to self-feeding which is the usual fledgling response to reduced feeding rates in other bird species (Davies, Behaviour 59:280–295, 1976).

Treatment values for RDPB (N/min) were compared at 12 days PH because all biologically important brooding observed in this study occurred then (Hitchcock and Mirarchi 1984). No differences ($P = 0.22$) in RDPB were observed between single parent (52.7 ± 14.8 [6]) and normal nests (69.6 ± 4.7 [54]). One single parent was observed brooding during the entire noon observation period (12:00–14:00) accounting for the lack of significant difference in brooding between treatments. Female Mourning Doves normally do not brood at this time (Taylor, M.S. thesis, N.C. State Univ., Raleigh, North Carolina, 1941; Harris et al., Am. Midl. Nat. 69:150–172, 1963) but appear capable of doing so when their mates are lost. This apparent ability to change incubation habits also has been reported in Ringed Turtle-Doves (*Streptopelia risoria*) (Wallman et al., J. Comp. Physiol. Psych. 93:481–492, 1979). This flexibility in brooding behavior is critical to Mourning Dove nestling survival under adverse weather conditions before homeothermy is achieved. Six fledglings (ages 14 days and younger), which had prematurely fallen from their nest during this and a subsequent study, were observed to die of exposure without consistent parental brooding (R. R. Hitchcock and J. B. Grand, unpubl.).

These observations demonstrate that wild, single-parent female Mourning Doves can care for their young PF by feeding and brooding them at times when normal female parent-fledgling interactions do not occur. However, the reduced number and duration of single-parent female feedings during the critical part of the fledgling dependency period indicates the possibility of slower development and increased mortality for single-parent fledglings. More extensive orphaning experiments should be combined with radiotelemetry studies during the fledgling dependency period to determine if differential rates of growth, development, and mortality are related to the sex of the parent removed and fledgling age class.

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Nest-sites of Turkey Vultures in buildings in southeastern Illinois.—Turkey Vultures (*Cathartes aura*) are known to nest in a variety of places: on the ground in thickets, under overhanging rocks or in caves, on exposed faces of cliffs, and in hollow trees, logs, and stumps (Jackson, J. A., pp. 247–270 *in* Vulture Biology and Management, S. Wilbur and J. A. Jackson, eds., Univ. Calif. Press, Los Angeles, California 1983), a pig-sty (Jackson, Bird-Lore 28:175–180, 1903), a tumbled-down house (Sprunt and Chamberlain, South Carolina

Bird Life, Univ. South Carolina Press, Columbia, South Carolina, 1949), and in barns (Pickens, Auk 44:573–574, 1927; Tyler, pp. 12–28 *in* Bent's Life Histories of North American Birds of Prey, Pt. 1, Dover Publ., New York, New York, 1961). Sample sizes were small or not mentioned by these authors.

In southeastern Illinois, Turkey Vultures were found commonly nesting in abandoned structures. From 1978–1983, 15 nests were observed and four others were reported by local farmers in the area. The 19 nests were situated in eight different barns, two old houses, and an old storage shed. No Turkey Vulture nests were discovered in natural sites during the 5-year period, but no intensive search for such nests was made. However, selection of abandoned buildings was evident as 70% of the structures checked during the study had nests. The decline in use of natural cavities for nest-sites by Turkey Vultures (Jackson 1983) may be related to this seeming shift by vultures to nest-sites in abandoned buildings.

All buildings were in or at the edge of wooded areas; all were abandoned except for the storage of farm equipment in some of the barns; and none was closer than 80 m to the nearest homestead. All 16 nests found in barns were in hay lofts. In the houses, one nest was on a first floor, and the other was on a second floor. The nest in the shed was on the ground.

Nests had been placed in dark corners of the building or in cavities created by spaces between bales of hay. Jackson (1983:264) also noted that Turkey Vulture nest-sites were typically in "dark recesses." Nest substrates consisted of wheat straw (N = 15), wood (N = 2), corn stalks (N = 1), and rotten wood (N = 1).

The history of two nests found in our survey was followed from initiation to fledging. The first eggs were layed on 29 April and 8 May, and hatched on 3 June and 11 June, respectively. Fledging occurred approximately 81 and 66 days later. One other nest contained one egg on 2 May, but was found destroyed 10 days later.

Fourteen of the 19 nests were successful, four were destroyed by predators, and one was destroyed when one of the houses was demolished. Nest destruction occurred only during egg-laying (N = 1) or incubation (N = 4). The nest success of 79.2% was higher than the 53.3% reported by Jackson (1983:262). Turkey Vulture eggs and nestlings in nests placed on the ground in thickets have higher mortality rates compared to nests above the ground (Jackson 1983). Since most of the nests in our study were in barn lofts, the nest success could be greater than in ground nests because predators such as coyotes (*Canis latrans*), red foxes (*Vulpes fulva*), and domestic dogs (*C. familiaris*) could not reach them.

Each completed nest contained two eggs. Of the 28 eggs of known fertility two were judged infertile when opened. In one barn, single nests over 5 consecutive years fledged a total of nine young.

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Nesting distribution and reproductive status of Ospreys along the upper Missouri River, Montana.—The enhancement and expansion of Osprey (*Pandion haliaetus*) habitat as a result of the construction of reservoirs has been noted in a number of sites in the western United States (Roberts and Lind, pp. 215–222 *in* Trans. N. Am. Osprey Resear. Conf., U.S. D. I., Natl. Park Serv., Trans. and Proc. Ser. No. 2, 1977; Henny et al., Northwest Sci. 52:

TABLE 1
SUMMARY OF OSPREY PRODUCTIVITY, UPPER MISSOURI RIVER

	1981	1982
No. occupied nests	38	45
No. active nests	29	36
No. advanced young	50	43
No. successful nests	22	21
No. advanced young/active nest	1.72	1.19
No. advanced young/occupied nest	1.32	0.96

261–271, 1978; Swenson, Western Birds 12:47–51, 1981). Here, I report on Osprey nesting along the upper Missouri River and compare nesting density on free-flowing and impounded portions of the river. As the two habitats abut one another and were studied concurrently, differences due to climate were minimal.

Study area and methods.—The area studied was in southwestern Montana, beginning at the headwaters of the Missouri River and ending approximately 190 km north at Holter Dam. The study area was divided into four segments: the free-flowing segment and three reservoir segments—Canyon Ferry Reservoir, Hauser Lake, and Holter Reservoir.

Nesting terminology follows that of Postupalsky (pp. 1–11 *in* Trans. of the N. Am. Osprey Resear. Conf., U.S.D.I., Natl. Park Serv., Trans. and Proc. Ser. No. 2, 1977) in which occupied nests are defined as nests that have a mated pair of Ospreys associated with them. An active nest is a nest that has had at least one egg laid in it. In this study a nesting attempt was considered successful if at least one young was raised to an advanced stage of development, i.e., at least to within 1 week of fledging. Seven aerial surveys were conducted over the 2 years of the study to locate occupied nests and to determine the productivity of the population. Dates of the flights were: 4 May, 22 June, and 31 July 1981; 15 May, 4 June, and 8 and 29 July 1982. Information from aerial surveys was supplemented by ground observations. Lengths of the reservoirs were estimated as the length of the river prior to impoundment. This method allowed for a measure of the impact of reservoir formation on nesting distribution, as one river segment was not impounded. Families of fishes taken as prey were determined by collecting the cleithra (external and adjacent to the clavicle) and

TABLE 2
NESTING DENSITIES AND DISTRIBUTION OF OSPREYS, UPPER MISSOURI RIVER, 1981–1982

Study area segment	Nest density (occupied nests/km)[a]	Mean no. occupied nests/year (%)
River	0.03	2.0 (4.8)
Canyon Ferry	0.41	26.0 (62.7)
Hauser	0.12	3.0 (7.2)
Holter	0.26	10.5 (25.3)
Total	0.22	41.5 (100.0)

[a] One by two contingency tables showed significant differences in occupied nests/100 km between the river and each of the reservoirs (all $P < 0.025$).

TABLE 3

NUMBER OF CLEITHRA AND OPERCLES COLLECTED FROM BELOW OSPREY NESTS AND FEEDING PERCHES ON THREE STUDY AREA SEGMENTS, UPPER MISSOURI RIVER, 1981–1982[a]

Family	Study area segment		
	River	Canyon Ferry	Holter
Sucker (Catostomidae)	155 (70)[b]	1710 (74)	702 (72)
Minnow (Cyprinidae)	42 (19)	107 (5)	51 (5)
Perch (Percidae)	1 (<1)	429 (18)	126 (13)
Trout (Salmonidae)	22 (10)	79 (3)	93 (10)
Total	220 (99)	2325 (100)	972 (100)

[a] Two by four contingency tables showed a significant difference between the river segment percentages and the Canyon Ferry percentages ($\chi^2 = 30.0$, df = 3, $P < 0.005$) and between the river and Holter ($\chi^2 = 21.2$, df = 3, $P < 0.005$) but not between Canyon Ferry and Holter ($\chi^2 = 4.62$, df = 3, $P = 0.21$).

[b] Percent of total.

opercles (large posterior bone of the gill cover) found below feeding perches and nests. Collected bones were then compared to a reference collection for family identification. Although the use of bones for determing food habits of Ospreys can be misleading (heavier boned fish tend to be overrepresented), their use for the purpose of detecting differences in diets should be valid.

Results and discussion.—The productivity of Ospreys in this study (Table 1) compares favorably with other western United States populations: 1.27 young per occupied nest in Idaho (Van Daele and Van Daele, Condor 84:292–299, 1982) and 0.60 young per occupied nest on Yellowstone Lake, Wyoming (Swenson, J. Wildl. Manage. 43:595–601, 1979).

The establishment of reservoirs appears to have increased nesting densities. The number of occupied nests per kilometer of river was significantly higher on the reservoirs than on the free-flowing segment of the river (Table 2). Newton (Can. Field-Nat. 90:274–300, 1976) stated that nest-sites and food are the chief factors governing the density of breeding raptors. My observations indicate that nest-sites are not limiting the distribution of Ospreys on the upper Missouri River (Grover, M.S. thesis, Montana State Univ., Bozeman, Montana, 1983). Table 3 depicts differences in the relative use of prey on three river segments. Perch were taken more often and minnows less often on the reservoir portions of the study area. These differences reflect changes in the prey species composition, changes in the prey species availability, or both, resulting from reservoir formation. These changes may then be making the reservoirs a more desirable nesting habitat by allowing the birds to more easily meet their energy demands.

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Molt in vagrant Black Scoters wintering in peninsular Florida.—The Black Scoter (*Melanitta nigra*) is a vagrant south along peninsular Florida, although it occurs regularly south to Jacksonville and St. Augustine on the Atlantic Coast (Bellrose, Ducks, Geese and Swans of North America, Wildlife Management Institute and Illinois Natural History Survey, Stackpole Books, Harrisburgh, Pennsylvania, 1976; Bancroft and Hoffman, in press, Fla. Field Nat.). An unusual influx of Black Scoters occurred during the winter of 1981–82, with birds recorded as far south as Fort Lauderdale on the Atlantic Coast and Naples on the Gulf Coast (Bancroft and Hoffman, in press). The bird collection of the University of South Florida (USF) received 15 Black Scoters (mostly immatures) during the course of the winter and spring.

Most of these birds were involved in molt of their head and body feathers, and their rectrices. Because the order of rectrix replacement seems not to be described adequately for any duck, we provide a description of the replacement of Juvenal with First Basic rectrices in these scoters. The pattern we found was complicated but fairly standardized, suggesting that the "irregular" replacement reported for other ducks (e.g., Weller, Wilson Bull. 69:5–38, 1957; Oring, Auk 85:335–380, 1968) deserves closer examination. We also describe the pattern of body molt for these individuals.

Methods.—All specimens examined were birds found sick on Florida beaches from November 1981 through May 1982. Fourteen specimens, all from Pinellas County beaches, were obtained from the Suncoast Seabird Sanctuary, a rehabilitation facility in Indian Shores, Pinellas Co. One specimen from Vero Beach, Indian River Co. on the Atlantic Coast, was delivered to USF by H. W. Kale II of the Florida Audubon Society. Where necessary, we refer to specimens by field catalog numbers of the preparators.

We follow Palmer (pp. 65–102 *in* Avian Biology, Vol. 2, Farner and King, eds., Academic Press, New York, New York, 1972) for terminology of molts and plumages. Palmer follows the Humphrey-Parkes (Auk 76:1–31, 1959) system of classifying molts and plumages, but presents a more detailed account of molt sequences in waterfowl. Names of feather tracts follow Lucas and Stettenheim (Avian Anatomy: Integument, Pt. 1, Agric. Handbook 362, Washington, D.C., 1972, Fig. 58, Figs. 88–94). Molt was recorded for six feather tracts from the head (frontal, coronal, loral, postauricular, malar, and submalar), two from the neck (dorsal cervical and ventral cervical), and eight from the body (pectorosternal, femoral, abdominal, humeral, interscapular, dorsal, pelvic, caudal). For active tracts we estimated the proportion of Juvenal feathers replaced. Wing tracts in scoters retain Juvenal feathers throughout the first winter (Palmer, Handbook of North American Birds, Vol. 3, Yale Univ. Press, New Haven, Connecticut, 1976), so are not considered further here.

Rectrix molt was easier to quantify than body molt. Except for the two November specimens, the Juvenal rectrices were extremely worn and easily distinguished from Basic rectrices. Black Scoters have 16 rectrices (Cramp et al., Handbook of Birds of Europe, the Middle East, and North Africa; the Birds of the Western Palearctic, Vol. 1, Ostrich to Ducks, Oxford Univ. Press, Oxford, England, 1977); we designated the rectrices on the left side L1 (central) through L8 (outer), and those on the right side, R1 through R8. We refer to pairs of rectrices, consisting of the equivalent feathers from the two sides, by their numbers. Because of extremely rapid rates of abrasive wear of the new Basic rectrices, the relative ages of these feathers could be determined after all had been replaced. We classified the Basic rectrices of the six birds in April and May with completed molt as worn (5) or fresh (6) to indicate relative ages of the feathers.

Ideally, body molt is recorded from live birds, fresh carcasses, flat skins (Humphrey and Clark, Condor 63:365–385, 1961), or during preparation of study skins (Dwight, Auk 31:

TABLE 1

RECTRIX MOLT OF BLACK SCOTERS OBTAINED IN FLORIDA BETWEEN NOVEMBER 1981 AND JUNE 1982

			Rectrices															
			Left								Right							
Bird	Sex	Date	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8
Specimens retaining at least some Juvenal rectrices																		
GEW 5445	M	9 Nov.	1[a]	1	1	1	1	1	1	1	1	1	1	1	1	1	2[b]	1
GTB 143	F	12 Nov.	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
WH 198	F	20 Feb.	2	2	2	1	1	1	1	3[c]	3	1	1	1	1	2	1	2
EBJ 15	M	6 Mar.	4[d]	3	3	1	1	1	2	4	4	3	1	3	1	3	2	4
WH 195	M	24 Mar.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
WH 197	F	31 Mar.	4	4	4	1	1	1	4	4	4	4	1	1	1	1	4	4
GTB 123	M	1–7 Apr.	4	2	2	4	1	3	4	4	4	4	3	3	2	4	4	4
Specimens with Basic rectrices only																		
GTB 124	F	6–10 Apr.	5[e]	5	5	5	6[f]	6	5	5	5	5	6	6	5	5	5	5
GTB 127	F	14 Apr.	5	5	5	6	5	6	5	5	5	5	6	6	6	5	5	5
GTB 125	F	6–15 Apr.	5	6	6	6	6	6	6	5	5	6	6	6	6	6	5	2
GTB 126	F	16–17 Apr.	5	5	6	6	6	6	5	5	5	5	6	6	6	6	5	5
WH 196	F	21 Apr.	5	5	6	6	5	6	5	5	5	5	6	6	5	6	5	5
WH 194	F	1 May	5	5	5	6	6	3	5	5	5	5	6	6	5	6	6	5

[a] 1 = Juvenal rectrix.
[b] 2 = rectrix missing.
[c] 3 = Basic rectrix partially grown.
[d] 4 = Basic rectrix fully grown.
[e] 5 = Basic rectrix worn.
[f] 6 = Basic rectrix fresh.

293–308, 1914). On dried study skins active papillae and partially grown feathers often are hidden under the fully grown feathers or under the wings and legs. Molt was recorded during preparation for six of the scoter study skins. We examined these specimens for sheathed and partially grown feathers, and for the characteristic blackish appearance of active feather papillae. Also, in most tracts replacement feathers could be distinguished from Juvenal feathers by differences in color and degree of wear. The capital and cervical tracts of juvenile females provided the greatest difficulties.

Of the other nine birds received, eight were prepared as study skins and one as a skeleton, before the significance of the molt patterns became evident. Before recording molt from the eight study skins, we restudied the six specimens on which molt had been previously recorded to determine how well molt could be detected and to cross-calibrate our determination of molt intensity. The primary external indications of molt were presence of sheaths on feathers, abnormally short feathers (incompletely grown), loose sheathed feathers in tracts, and loose detritus of feather sheaths among feathers. The last two indicators tended to be lost during examination.

We were able to detect molt reliably on the study skins for all head and neck tracts, and for body tracts except dorsal, pelvic, crural, and ventral portion of the caudal (under tail coverts). These tracts generally were hidden beneath the wings or feet. Molt was then recorded

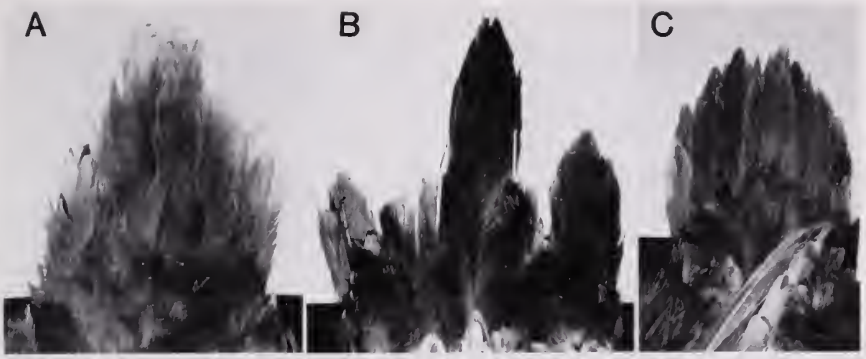

FIG. 1. Tails of Black Scoter specimens, dorsal view. A. GTB 143 from 12 November. All rectrices are Juvenal. B. WH 197 from 31 March. Seven Juvenal rectrices remain as bare shafts. The other nine are replaced by fully grown first-basic rectrices. C. GTB 125 from 6–15 April. All rectrices are Basic. The innermost and outermost are moderately worn and appear paler.

for the 14 remaining tracts on seven of the eight study skins (the eighth was an adult male which was not in molt). Molt data were not recorded on the immature male prepared as a skeleton.

Patterns of rectrix molt.—The Juvenal rectrices have notched tips (Palmer 1976:310) and have a narrower rachis (M. Weller, pers. comm.), whereas subsequent feathers taper to pointed tips. However, on our specimens the Juvenal rectrices generally were abraded so severely that notches were not evident.

The sequence of rectrix replacement was complicated and variable (Table 1). The innermost pair and outermost two or three pairs were replaced first and more or less simultaneously. On some specimens, pair 2 was replaced at about the same time. The remaining pairs 2 or 3 through 5 or 6, were dropped after the innermost and outermost pairs were completely grown. The order among pairs 3–5 was highly variable, but often pair 3 was replaced last.

On both November specimens the rectrices present were Juvenal and moderately worn (Fig. 1A). These specimens still show the notched tips typical of Juvenal rectrices. Four specimens from February–April were in intermediate stages of rectrix molt. One (WH 197; Fig. 1B) had seven Juvenal and nine fully grown Basic rectrices, and apparently was not in active tail molt at the time of death. Note that the Juvenal rectrices are extremely worn, and only stubs of the shaft remain. Note also the pointed tips of the Basic rectrices.

The females from April and May apparently had completed tail replacement, although one (WH 194) was growing rectrix L3. Another (GTB 125) lacked R8, but we suspect accidental loss of this Basic feather. The least worn (hence youngest) rectrices were in pairs 3–5, and pairs 1 and 8 were always worn (Fig. 1C). The patterns of wear on these birds suggest (as does WH 197) a two-stage replacement of the tail. Pairs 1 and 8 are replaced early and nearly synchronously, usually along with pairs 2 and 7 and sometimes feathers from pairs 4 and 6. The remaining rectrices are replaced rather quickly but apparently after a hiatus in molt.

Patterns of head and body molt.—Like Palmer (1976:309–311), we were unable to separate satisfactorily the First Basic and First Alternate feather generations on the head and body,

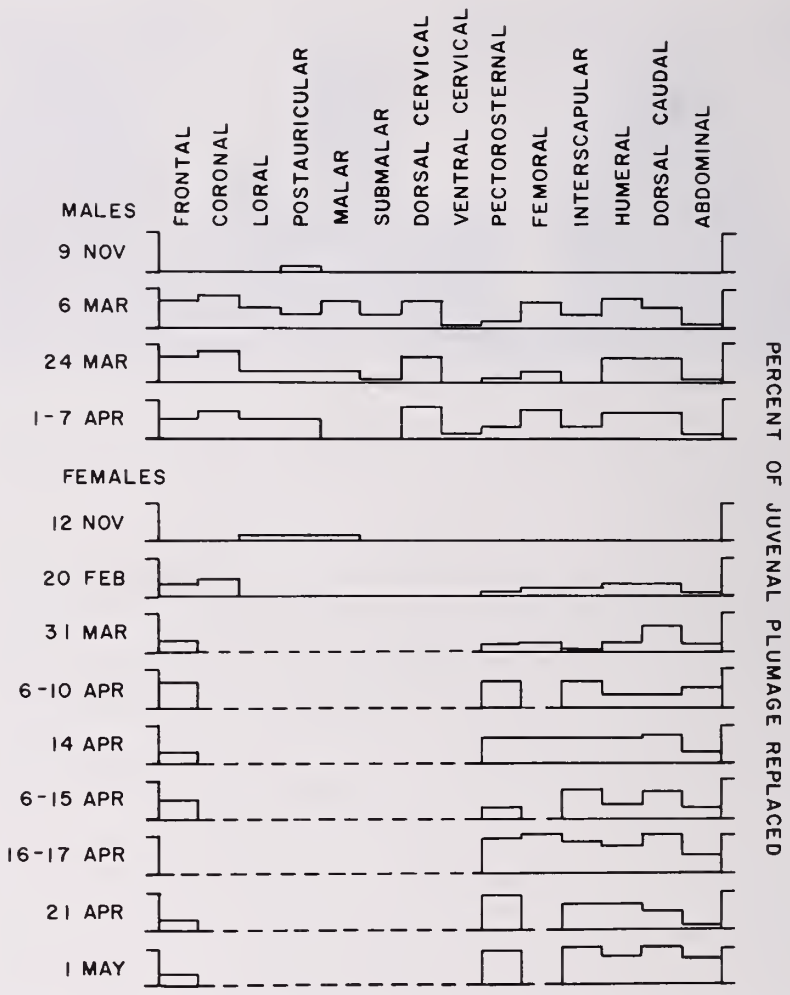

FIG. 2. The extent of plumage replacement for 14 head and body tracts. The bars indicate percentage (0–100) of Juvenal plumage in each tract replaced by Basic and Alternate feathers. Dotted lines indicate tracts that could not be scored on particular specimens.

in part because we lack specimens from December and January. Palmer also reported that Black Scoters have a First Basic plumage of "all feathering except wing" attained usually in fall, and a First Alternate plumage including all feathering "except wing and tail" acquired in late autumn. The timing of molt in Florida specimens was later, perhaps abnormal. Even so, a description of the patterns of feather replacement seems useful in further understanding the sequence of feather replacement in scoters and in understanding factors that influence the timing of molt.

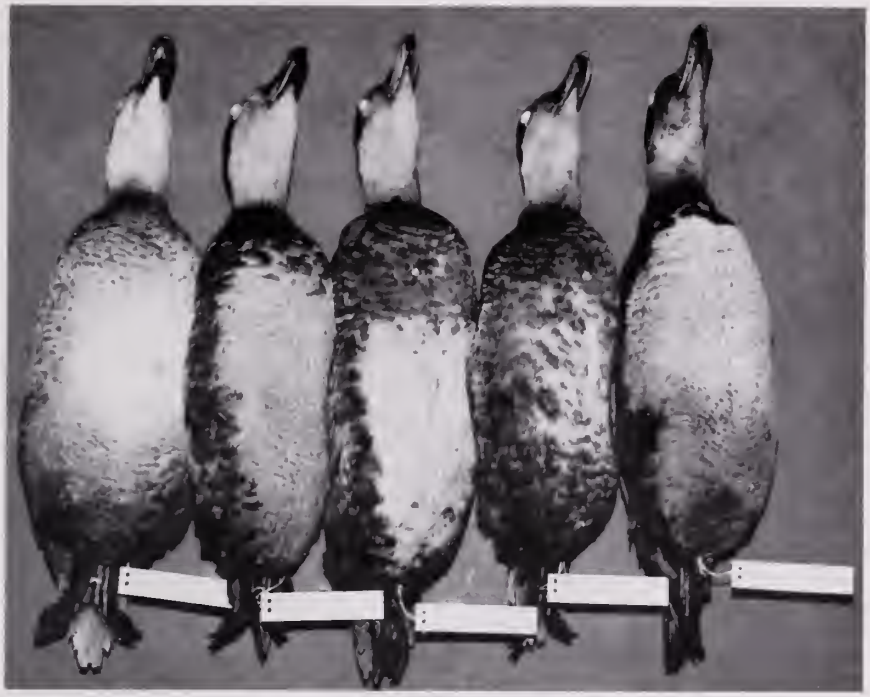

FIG. 3. The course of feather replacement in the ventral tracts in female Black Scoters. The right most bird is a male (EBJ 15, 6 March) for comparison. Females, from left: GTB 143, 12 Nov.; WH 197, 31 March; GTB 124, 6–10 April; WH 194, 1 May.

Fig. 2 illustrates the percentage of each tract containing new feathers (Basic or Alternate) rather than Juvenal feathers. Because of color differences, replaced feathers were quite apparent on males for all tracts considered. On females, fully grown replacement feathers could not be distinguished from Juvenal feathers on most of the head and neck tracts. The differences in color of the Juvenal feathers in the pectorosternal tract result from differential wear and fading.

Molt began in the post-auricular and loral tracts (November specimens) and then spread over the head and on to the body. Dorsally, the humeral and femoral tracts were activated well before the interscapular tract, at least in males. Within the pectorosternal tract the pattern of feather replacement was quite consistent (Fig. 3). Molt appears at the anteromedial margins of the tract, then spreads back along the lateral margins. Feather replacement moves in a wave posteriorly and medially. The abdominal tract lags behind most other body tracts.

In Fig. 2, the relationship between date and stage of molt is much weaker than expected. The three males from March and April died at essentially the same stage of molt. Among females, little progress is evident in molt of the frontal, humeral, or dorsal-caudal tracts between 20 February and 1 May. The individual from 21 April (WH 196) in particular shows little progress beyond the stage shown in February.

We suspect that these birds, attempting to winter south of their normal range, were

physiologically stressed and so delayed molt (Bancroft and Hoffman, in press). When they did begin molt the additional stress probably contributed to their death.

Discussion.—The pattern of rectrix molt we describe in Black Scoters is fairly complicated, and enough variability is present even in our limited sample, that the pattern could have been dismissed as "irregular" (e.g., Weller 1957, Oring 1968). Our data suggest the order of rectrix replacement in ducks in general deserves closer examination.

The timing of the first Prebasic and First Prealternate molts in the Black Scoter is the subject of some controversy. Palmer (1976) indicates that Black Scoters attain their First Basic and First Alternate plumage in autumn, but Cramp et al. (1977) report that immatures in Europe are molting from September through May with a very incomplete post-juvenal (=First Prebasic) molt in fall followed by a protracted prenuptial (=First Prealternate) molt. Apparently our understanding of scoter molt has advanced little during the seven decades since Dwight (1914) first discussed the subject! Dwight stressed the great individual variation in timing of molt in his specimens but because they apparently were collected in various locations over a number of years, the meaning of this variation is unclear.

Our specimens seem to fit better the molt patterns described by Dwight (1914) and Cramp et al. (1977) than those described by Palmer (1976), but our sample may be biased. Clarification of this issue will likely require adequate series of healthy Black Scoters collected within the normal winter range.

Acknowledgments.—L. A. Hanners, E. B. Jones, K. J. McGowan, S. R. Patton, and G. E. Woolfenden read and improved an early version of the manuscript. A. M. Bancroft, E. B. Jones, and G. E. Woolfenden prepared some of the study skins. K. C. Parkes and M. W. Weller made numerous constructive comments on a later version of this paper. We thank all the above people.—Wayne Hoffman and G. Thomas Bancroft, *Dept. Biology, Univ. South Florida, Tampa, Florida 33620.* *Accepted 14 Feb. 1984.*

GEORGE MIKSCH SUTTON AWARD FOR ORNITHOLOGICAL ART

The Wilson Ornithological Society announces the establishment of the George Miksch Sutton Award for Ornithological Art. The Award will be given for art that would be suitable as a color plate in The Wilson Bulletin. The subject matter and medium are at the artist's discretion. Size of the artwork should be no smaller than 9¼ wide × 14 inches high and no larger than 18⅜ × 27¾. Any artist who has not been represented by a major gallery or who has not been featured in magazines such as Audubon or National Wildlife is eligible to enter. Prior publication of a color plate in a professional journal does not disqualify an artist. In short, the competition is primarily for artists who do not make their living, or a significant portion of it, by painting birds. Artists who question their eligibility should query the Award Committee when requesting entry information. Artwork will be judged by a panel of ornithologists and artists at the June 1985 Wilson Ornithological Society/Cooper Ornithological Society joint annual meeting in Boulder, Colorado. All qualified entries will be on display at the meeting. Artists should insure their entries both to and from the meeting and include a return mailer with postage attached. Matting and/or framing is at the discretion of the artist. The winner of the competition will receive a check for $500, and his/her artwork will appear as a color plate in The Wilson Bulletin. For further information and application form, contact **Phillips B. Street, Chairman, Sutton Award Committee, Lionville Station Road, R. D. 1, Chester Springs, Pa. 19425.**

Wilson Bull., 96(3), 1984, pp. 505–513

ORNITHOLOGICAL LITERATURE

THE LIFE AND LETTERS OF ALEXANDER WILSON. By Clark Hunter (ed.). American Philosophical Society, Philadelphia, 1983:456 pp., 21 figs., 3 maps, 4 color plates. $40.00.—The last major biographical work on Alexander Wilson, by Robert Cantwell, appeared nearly a quarter of a century ago and is still considered the definitive Wilson biography. The present work is not intended to supersede Cantwell's effort, but rather to be vehicle for bringing forth about 40 of Wilson's unpublished letters and gathering in one place over 100 additional letters previously published in scattered sources over the last 160 years. Many of the latter had been altered by contemporary editors squeamish about naming names, and they appear unadulterated here for the first time. Hunter's life of Wilson occupies about 100 pages of the volume and is offered, as the author avows, as an explanatory companion for the real stuff of this work, Wilson's own letters. Included in the four appendices are Wilson's United States naturalization certificate, his last will and testament, and the court records from a political scandal that Wilson brought upon himself in his native Paisley, Scotland, prior to his departure for America.

Clark Hunter, himself a Scotsman, confesses to being a bibliophile rather than an ornithologist. The book is a scholarly work, however, and a relatively modest production, although the somewhat steep price is partly a reflection of the book's high quality paper and antique type face. The annotations of the letters might appear to leave something to be desired in their quantity, but this I believe to be due not to any lack of zeal on the editor's part, but rather to the difficulty in securing accurate information. It is nearly 200 years since some of these letters were written, and time and the overprotectiveness of Wilson's earliest biographers have done much to conceal facts from the modern editor. Hunter has done admirably in the face of these obstacles. In general the letters require little comment; such passages as this one, in a letter to William Bartram in 1804, speak volumes about the milieu in which Wilson worked: "I have been drawing Woodpeckers this sometime. Pray be so good as inform me if there is not 4 different species besides the Flicker in these parts . . . . I suppose that none of the large red Crested Ones can be found within 20 miles of Philada I would not begrudge 2 days sacrificed in getting possession of One." An ornithological editor might, however, remark on the following passage from the same letter: "I lately discovered a new and most extraordinary Blackheaded Woodpecker on the trunk of a large tree in your [eastern Pennsylvania] woods of a perfect nondescript species. The largest of my Hawks was a mere Tom Tit to it . . . . [W]ith what Genus to class it I am totally ignorant. One thing I am positive of, that it was a *Woodpecker,* a *black-headed* one and a very expert one too." The identity of such an extraordinary beast is a mystery.

I did object to the absence of a means of readily determining which were the previously unpublished letters, and would have liked to know the source of a quotation from Daniel Defoe on page 19 and the identity of "a bird previously undescribed by naturalists," mentioned on page 77. The reference on page 90 to Charles Willson Peale as the founder of America's first natural history museum would be more meaningful if it were also noted that that museum was the Philadelphia Academy. Such criticisms aside, this book is an important one for scholars interested in Alexander Wilson's life in particular and for anyone interested in the history of American ornithology in general.—MARY C. MCKITRICK.

THE FEEDING SYSTEM OF THE PIGEON (*Columba livia* L.). By Gart (A.) Zweers. Advances in Anatomy, Embryology, and Cell Biology, Vol. 73. Springer-Verlag, Berlin, Heidelberg,

New York, 1982:vii + 108 pp., 45 numbered text figs., 3 tables. $26.00.—Avian feeding adaptations have always held a special fascination for ornithologists because of the seemingly unlimited variety of bill shapes, diets, feeding behaviors, and feeding strategies in birds. It is, therefore, remarkable that today still relatively little is known about the functional anatomy of the avian feeding apparatus. Though the continuous trickle of publications dealing with some aspects or the other of the anatomy of the avian feeding system had never completely ceased to flow, more functionally oriented studies on a variety of species started to appear at an increasing rate during the past two decades.

Gart Zweers has been working for more than a decade on the anatomy of the avian feeding system in relation to feeding and drinking adaptations, and the pigeon (*Columba livia*) represents the second species for which he has produced extensive and detailed data on the functional anatomy of the feeding system. His previous work on the Mallard (*Anas platyrhynchos*) (Zweers, Netherl. J. Zool. 24:323–467, 1974; Zweers et al., Contributions to Vertebrate Evolution, Vol. 3, Karger, Basel, New York, 1977) focused on functional-morphological aspects of the jaw and lingual apparatus, whereas his work on the pigeon (see also Zweers et al., Zoomorphology 99:37–69, 1981; Zweers, Behaviour 80:274–317, 1982) has dealt so far with the functional morphology of the tongue, larynx, and mouth cavity. (The morphology of the pigeon jaw apparatus was recently studied by Bhattacharyya, Proc. Zoo. Soc. Calcutta 31:95–127, 1980.)

Zweer's approach is typical of that of the "Leiden school of morphology" in which not only selected structures of a system are studied (e.g., muscles and bones) but in which the structural elements are viewed as parts of a whole system (e.g., tongue). Several such systems, in turn, interact with one another and are responsible for the integrated functioning of the entire organism. With this approach, detailed anatomical descriptions and functional interpretations of the structures are of special importance. Zweer's work is characterized by this and by state-of-the-art electrophysiological techniques.

The volume consists of three parts. "Part 1: The lingual apparatus" is a macroscopic description of the surface structures, orifices of the salivary glands, skeletal elements, articulations and ligaments of the hyoid, and of the lingual extrinsic and intrinsic musculature. The description of the surface structures and salivary glands is very brief and relies heavily on literature references; the other structures are treated in greater detail. The nomenclatures suggested by different authors for the salivary glands, hyoid skeleton, and lingual muscles are synonymized. The table on muscle terminologies is extensively annotated.

In "Part 2: The mouth and pharynx," the shape of the buccal and pharyngeal cavities and the histology of the tongue and surface structures are described with the help of 17 figures representing cross-sections through the palatal region, lower mandible, tongue, and larynx in situ. Larger nerves and blood vessels are also described here. This type of anatomical description allows the assessment of the relative positions of the various components of the feeding apparatus but is not conducive to arriving at a three-dimensional visualization of the anatomy of the feeding system.

In "Part 3: Mechanism of the feeding system," the anatomical structures described in parts (1) and (2) and functional studies from slow-motion cinematography and radiography and from electromyography are combined to formulate three models describing the functioning of the feeding systems. (1) The "slide-and-glue mechanism for pecking" explains how seeds are picked up by grasping them between the upper and lower mandibles and transported into the buccal cavity by gluing them to the sticky tip of the retracting tongue. Larger seeds are swallowed by a "catch-and-throw" mechanism. (2) As a drinking method, a "double-suction mechanism" is proposed in which capillary action is responsible for bringing water between the slightly gaping tips of the beak and in which the tongue acts as a piston to pump the water into the pharyngeal cavity. No peristalsis of the esophagus is

observed during drinking. (3) The "drill-chuck mechanism" of the larynx is a model describing the opening and closing of the glottis.

Due to its clear organization, broad range of topics, and extensive bibliography, this paperback booklet (the binding is excellent!) will be of interest to ornithologists working on the behavior and ecology of drinking and feeding in birds in general and to those studying pigeons. It is of special interest to avian functional morphologists, and should be acquired by university libraries as a useful reference.—Dominique G. Homberger.

Dorsal Ventricular Ridge: A Treatise on Forebrain Organization in Reptiles and Birds. By Philip S. Ulinski. John Wiley & Sons, Inc., New York, New York, 1983:284 pp., 114 numbered text figs. $39.95.—The dorsal ventricular ridge (DVR) of the reptilian and avian brain is involved in the control and modulation of complex and "subtle" behaviors, and is comparable to much of the cerebral cortex of mammals. As such, it demands the attention of those interested in understanding the neural basis of animal behavior, especially more intricate behavior such as singing in birds. Recent technical advances in tracing neural connections within the brain have led to a great increase in information on forebrain structure in reptiles and birds, and Ulinski has accumulated and organized these data to provide the first comprehensive treatment of the morphology, physiology, and functional significance of the DVR. While a major goal of the author is to formulate a paradigm to help guide further research on the DVR, the book also summarizes the available information and presents it in a way that any biologist can appreciate. The result is a book that is essential for neuroscientists dealing with this or related systems, and also useful for anyone interested in keeping up with advancements in the melding of brain and behavior.

The book basically has two components: a major part devoted to an exhaustive (and to the non-specialist exhausting) review of the structure and physiology of the DVR, and a briefer section devoted to consideration of more general functional and evolutionary aspects of the system. The main purpose of the first part is to define exactly what the DVR is and to then relate it both structurally and functionally to the rest of the nervous system. Information on the development, morphology, and physiology of both the DVR and brain systems which project to or receive projections from the DVR is included. Fortunately for the ornithologist, birds have received a fair amount of attention and avian studies are well represented. The treatment is detailed and the non-specialist may stagger under the weight of the neuroanatomical terminology, but summary sections in the last chapter are a consolation to any such victims. The text is clearly written, logically organized, and illustrative figures plentiful.

While the accumulation and integration of all pertinent data is clearly a boon to the neurobiologist, the conceptual framework provided in the last chapter is the boon for the general zoologist. Here the author considers the significance of the DVR in the most basic sense, as a linkage between sensory input and motor control that allows the proper expression of complex behavior. Included in the chapter is a discussion of evolutionary aspects of the DVR. The amount that can be said without resort to rampant speculation is limited, however, and comparative biologists have to take what they can get. (The presence of two fundamental patterns of DVR organization, one observed in snakes, lizards, and turtles, and the other in crocodilians and birds (and archosaurs?) may have some phylogenetic relevance.) Significantly, evolutionary speculation is centered on a coherent discussion of the hazards and difficulties of establishing structural homologies. The author is more interested in understanding the DVR in a functional sense, and comparing it to other systems that serve the same function. In this case, the analogous system is the well-studied isocortex of the mammalian cerebrum, and while both have similar general functions, pronounced differences in

certain aspects of design demand explanation. Any complete explanation is relegated to the future after more work (especially physiological) is done on the DVR, but Ulinski at least has set the stage by skillfully formulating what may be the pertinent questions to ask.—Thomas E. Hetherington.

Population Ecology of the Dipper (*Cinclus mexicanus*) in the Front Range of Colorado. By Frank E. Price and Carl E. Bock. Studies in Avian Biology No. 7, Cooper Ornithological Society, 1983:84 pp., 20 numbered text figs,19 tables. $9.00.—The principal objective of this study by Price and Bock was to assess factors that influence the dynamics of Dipper populations. To this end, they spent 2½ years observing marked populations of birds in two creek drainages in the Front Range of the Colorado Rocky Mountains, collecting year-around data on individual movements, density, and dispersion, estimating annual survival and productivity, and measuring a variety of habitat attributes (biotic and abiotic) thought to affect all of the above.

Perhaps the salient feature of this research is its demonstration of the enormous advantages that can come when one has most of the members of a group individually marked (here, over 550 birds). Indeed, virtually all their information on dispersion, movement, territoriality, recruitment, and survival (much of which was in contradiction to previous assumptions about Dippers) could not have been obtained otherwise. Besides being easy to catch and mark, other features of Dipper biology render them convenient organisms for population studies, and each is exploited by Price and Bock in their sampling. This leads to the strength of the monograph: its breadth. Very few attributes that might affect the number of Dippers in the study area have been overlooked. Rather than focusing on only one or a few processes that might be important in regulating population size (e.g., competition, food resources, nest predation), they attempt to examine a wide variety. Predictably, their conclusions parallel those of similar broad studies of other species; even in a relatively simple system, a large number of processes interact in a complex manner to produce population dynamics.

Unfortunately, their breadth comes at the sacrifice of depth, which is particularly apparent in the relatively short duration of the study. They share this weakness with the majority of population studies: the phenomena they wish to address simply cannot be thoroughly assessed over a time span that includes just two annual population cycles.

Nonetheless, this study paints a broad picture of factors likely to be important in determining Dipper numbers. Given the relative simplicity of the system and the ease with which many of the salient features may be sampled, one can hope that Price and Bock's data form the basis for long-term observations of what ultimately could prove to be a model species.—John T. Rotenberry.

Estrildid Finches of the World. By Derek Goodwin. British Museum (Natural History), Comstock Publishing Associates, a division of Cornell University Press, Ithaca, New York, 1982:328 pp., 8 color plates by Martin Woodcock. $45.00.—This is an excellent volume on a very colorful family of birds. For years estrildids have been popular as cage birds, partly due to the ease with which they are bred in captivity, and a book that examines them from a distributional, behavioral, and nomenclatural standpoint is a welcome addition to the literature. In his introduction Goodwin discusses, among other things, the relationship of the whydahs and indigo-birds (*Vidua* spp.) to the estrildids. The whydahs and indigo-birds are brood parasites of estrildids. Traditionally two separate families are recognized, Ploceidae and Estrildidae, and the placement of the viduines then becomes a problem. The author notes that Delacour, Mayr, and Nicolai have demonstrated that each viduine closely

resembles in some way only one particular estrildid, namely its host. Goodwin therefore suggests that the viduines are to be "rightly included in the Ploceidae." Later he states (p. 8) that the book "does not include any detailed anatomical descriptions or voice analysis but references to work on those subjects are given where possible." Unfortunately it is information from anatomical disciplines such as osteology, myology, and pterylosis that provides conflicting evidence. In a classic paper Sushkin (1927, Bull. Am. Mus. Nat. Hist., 57:1–32) found *Vidua* and *Steganura* to be the most primitive of all Estrildinae on the basis of cranial osteology. Bentz (1979, Bull. Carnegie Mus., 15:1–25) on the basis of appendicular myology found *Vidua* to more closely resemble the Estrildidae than the Ploceidae. Friedman (1960, Bull. U.S. Natl. Mus., 223:VIII + 1–196) also considered the viduines to be more closely related to the estrildines. Thus it seems probable that the rightful placement of the viduines is with the estrildids. At any rate this has little to do with the book's main objective. Also included in the introduction is a concise and thorough characterization of the family Estrildidae.

Chapter 1 (2 pp.) deals briefly with nomenclature and describes how the estrildids are treated as a separate family, Estrildidae, rather than as a subfamily, Estrildinae, of the family Ploceidae. Goodwin simply mentions the use of tribes and rightly states that the genus is of greater concern to the non-taxonomist. He states that as far as possible he has adhered to the genera as they are listed in Peters' "Check-list of Birds of the World." Bentz (op. cit.) pointed out that Peters (Vol. 14, p. 306) subdivided the Estrildidae presumably into "tribes," but without the proper tribal termination -ini (Estrildae, Lonchurae, Poephilae) without it having first been divided into subfamilies. Again this is a small point.

Chapter 2 (3 pp.) deals briefly but adequately with the distribution and adaptive radiation of the group. Chapter 3 (3 pp.) discusses plumage and coloration.

One of the longer and more informative sections is Chapter 4 (31 pp.) on behavior and biology. This chapter includes such topics as feeding habits and bathing, anting and preening. Most estrildids feed on the seeds of grasses and all estrildids bathe in water and none dust bathe. This chapter also discusses behavior of the young and nest-decorating. Young estrildids beg for food with their head and neck supinated at an angle that ranges from 90–160 degrees and they only receive food that has first been swallowed by the parent. Also, many species of *Estrilda* build accessory nests on top of or along side the main nest. These "cocknests" are often decorated with bits of paper or white feathers. According to Goodwin, such nests serve to deceive predators and thus distract them away from the main nest below. Much has been written about the spotted and colored mouths of estrildid nestlings. In this regard Goodwin cites an interesting article by Swynnerton (1916, Ibis, 10th series, 4:264–294). Swynnerton had apparently been told by an African native that while adults of certain species of small passerines were quite tasty when eaten, their young were most unpleasant tasting. Brightly colored mouths of nestlings therefore might function as warning coloration. A detailed section on display and social behavior points out the vast amount of information that can be gained by careful and persistent observation of birds in captivity. The contribution of aviculturists in this regard has been great. So substantial has that contribution been and so popular are these birds as pets that the next chapter (5, 14 pp.) is devoted to estrildids in captivity.

Chapter 6 (255 pp.) discusses the species of estrildids. For each, the common and scientific names are given, as well as a range map. In addition each species is discussed with respect to field characters, distribution and habitat, feeding and general habits, nesting, voice, display and social behavior, and other names. This chapter also contains the color plates which are of good quality. Indices of common names and scientific names are provided.

This book is thorough and attractively priced. As such it will undoubtedly be of great use to both professional ornithologists as well as aviculturists.—Gregory Dean Bentz.

BREEDING BIRDS OF ONTARIO: NIDIOLOGY AND DISTRIBUTION. VOLUME 1: NONPASSERINES. By George K. Peck and Ross D. James. Royal Ontario Museum Life Sciences Miscellaneous Publications. Toronto, Canada. 1983:xii, 321 pp., 3 maps of regions and localities, 139 range maps, 42 figs. of habitats and some species. $25.00.—For each of the nonpasserine birds for which at least one nest has been found in Ontario, there is a range map and a descriptive text on the opposite page. Different symbols have been used to indicate if the records are recent or historical and whether they have been documented by collection or photography, or are based on sight records. For southern Ontario, the symbols are given by counties but in the north where the administrative districts are very large, the actual localities have been mapped. There is an introductory section on methods, an index of species names, a short bibliography, and a longer section on literature cited and acknowledgments. My only criticisms are somewhat trivial: burying the map symbols on page 9, inserting the illustrative figures after the index, and the somewhat incomplete citations in the bibliography and literature cited sections.

Both authors have done extensive field work in most regions of Ontario and have contributed photographs illustrating this work. Since 1966 the senior author has published an annual summary of the nest record results for the preceding year, but here for the first time range maps have been given and a summary of the total number of nests reported, the number of provincial regions represented, the habitats preferred, the character of the nests, the numbers in each clutch-size category, the range of egg dates, and, if known, the incubation period. The junior author has provided a number of sketches of some of the species mentioned. This is an important reference work for anyone interested in the nesting habits and distribution of birds.—J. MURRAY SPEIRS.

A GUIDE TO BIRD BEHAVIOR. VOLUME II. By Donald W. Stokes and Lillian Q. Stokes. Little, Brown, and Company, Boston, 1983. 334 pp., numerous line drawings. $14.95.—This book is a companion volume to D. W. Stokes' *A Guide to the Behavior of Common Birds,* which has now been renamed *A Guide to Bird Behavior, Volume I.* Together, the two volumes seek to promote "a new approach to birdwatching," one that stresses "observing what birds do rather than simply identifying them." To this end, the authors provide descriptions and interpretations of some basic behavior patterns for 50 species of North American birds, 25 per volume. The information presented in these books is accurate and well organized, the writing is concise and lucid, and in sum the authors deserve to succeed in their admirable purpose.

Both volumes are broken into 25 sections, each dealing with the behavior of one species. An index on the inside cover allows quick access to the desired species account. The bulk of each section consists of the "behavior descriptions," narratives that describe territory, courtship, nest-building, breeding, plumage, and seasonal movement. Additional subsections on flocking and feeder behavior are added where appropriate. These narratives describe the sorts of behavior a birdwatcher is likely to see, and provide information on the function of the behavior in the life of the bird. The behavior descriptions are supplemented by a "behavior calendar," which shows the months during which various categories of behavior can be seen, and by a "display guide," which gives fuller descriptions of some of the principal visual and auditory displays of the species. By reading the behavior descriptions, and making occasional reference to the display guide and behavior calendar, the reader should be able to categorize and understand most of the behavior he observes in a particular species. The volumes are compactly and sturdily bound for field use.

The authors have done a praiseworthy job of familiarizing themselves with the scientific literature on the species they cover, and of abstracting the important information on be-

havior. There are occasional oversimplifications and omissions; for example, in the section on Red-winged Blackbirds (*Agelaius phoeniceus*) (in Volume I), polygamous females are said to defend subterritories on the territory of the male, which is or ought to be controversial, and no mention is made of the use of multiple song types by the males. On the other hand, a degree of oversimplification is inevitable, given the task of describing a species' behavior in so short a space. Some of the treatments are actually quite sophisticated, as in the discussion of variation in mating system according to habitat in the Brown-headed Cowbird (*Molothrus ater*) (in Volume II). This and others of the species accounts employ the results of very recent scientific studies. Species were chosen for coverage based on the conspicuousness of their behavior; the choices are reasonable ones, though West Coast readers should be warned that a number of exclusively eastern birds are included.

Now that we have one, the need for a field guide to bird behavior is apparent. It seems a natural, and healthy, development for birdwatching to move beyond simple counting of species towards fuller observation and understanding of what birds are doing, and a book such as this is essential in promoting this development. Donald and Lillian Stokes are to be commended, both for the inspiration to produce a field guide to bird behavior, and for producing such a fine one.—William A. Searcy.

Enjoying Ornithology.—Edited by Ronald Hickling. T. and D. Poyser, Calton, Staffordshire, England (dist. in U.S.A. by Buteo Books, Vermillion, South Dakota 57069), 1983: 296 pp., 39 figs. $30.00—We have no census to prove it, but few of us doubt that Britain has the densest population of bird watchers in the world. It was to mobilize this enormous enthusiasm and talent constructively that the British Trust for Ornithology was formed in 1933. It was appropriate, therefore, that on the fiftieth anniversary of its founding the Trust should have sponsored a report on the progress of British Ornithology through cooperative projects, mainly by amateurs, during this century.

Very early the Trust chose its niche, namely, to gather facts about the birds of the British Isles at large. It has deliberately avoided dispersing its efforts into fields preempted by other established societies such as the British Ornithologists' Union (general ornithological science), the Royal Society for the Protection of Birds (conservation), the Wildfowl Trust (wildfowl preservation and research), and regional societies (local topics). Its journal, Bird Study, started in 1954, has consistently reflected this scope.

In many respects the Trust continues to serve as a model for the rest of the world. It has wedded the enjoyment of birds, as indicated in the title of this book, with ornithological science to yield unparalleled results. For example, it has managed all bird banding for the nation since 1937; it has coordinated visual and radar observations of migration; with the aid of more than 10,000 participants, it has completed the "Atlas of Breeding Birds of Britain and Ireland," and "Bird Habitats in Britain," the first such works of their kind; it continuously monitors populations through its Common Birds Census; it amasses vast stores of information in its Nest Record Scheme; and along the way it has sponsored and published the results of more than 150 specific studies. As we marvel at these accomplishments, we note the central role played by amateurs. Although professional help has been used, and financial support has come from grants and research contracts, the millions of hours of field and office work could not have been hired. Bird banders individually pay for the privilege. Even construction work at the headquarters was donated. The Nature Conservancy Council has been a consistent source of support through research contracts, but the Trust has never had a financial "angel" to guarantee its survival.

E. M. Nicholson, one of the founders, was invited to speak at the 1980 American Ornithologists' Union meeting in Fort Collins, Colorado, and J. M. McMeeking, then president

of the Trust, gave the keynote address at a special Cornell Laboratory meeting in 1978 on the amateur role in ornithology.

This book is much more than a history of the British Trust for Ornithology. Its chapters were contributed by a score of authors, each recounting aspects in which he was involved. Major sections deal with conservation, the role of sister organizations, and environmental problems in different habitats. Nearly 40 pages of facts and figures summarize important data gathered to date: banding recovery rates, longevity, causes of mortality, population densities, weather records, and bird weights. Many of these facts are not readily available elsewhere.

This report should be required reading for people organizing cooperative projects or searching for topics suitable for amateur research. American readers, however, may find some portions a bit parochial. The frequent use of initials to refer to organizations and projects may be like ABC to British readers but a challenge to the memories and ingenuity of the rest of us. Reading these pages and scanning the references, one gains little inkling of similar projects and environmental concerns elsewhere in the world. Yet, I cannot with good grace accuse the Trust of insularity after the Nest Record Scheme adopted my method of calculating nest success from fragmentary data, and its Common Birds Census adopted my device, a population index for tracing long-term trends from a changing sample base.

It is surprising to note how slight has been the involvement of the British Ornithologists' Union in all of these affairs. It does not even appear in the index. Indeed, a more detailed index would have been helpful, since many people will use this book by dipping into it for special topics. The Trust's own journal and other British journals are not listed. It is not obvious how the references in the published list were selected, since they are not cited specifically in the text.—Harold F. Mayfield.

America's Favorite Backyard Birds. By Kit Harrison and George Harrison. Simon and Schuster, New York, 1983:288 pp., 10 color plates, 188 black-and-white photographs, 10 line drawings, appendix, glossary. $15.95—Using simple language and abundant photographs, the Harrisons present basic phenology and behavior for 10 common, widespread, "backyard birds," a chapter apiece. Eight of the species occur on both coasts, but two, the Blue Jay (*Cyanocitta cristata*) and Northern Cardinal (*Cardinalis cardinalis*), are essentially eastern. Close relatives of featured species are also discussed and illustrated, and a closing chapter briefly surveys a variety of other common backyard birds. The glossary summarizes plants used for food, roosting, and nesting by each featured species.

For those with little or no formal knowledge about birds, this should be an extremely informative and enjoyable book. A surprising breadth of avian natural history is presented in an easy conversational tone that does seem to convey the spirit of the species. Frequent anecdotal reference to the observations of ornithologists lends a scientific credence, and gives something of the air of a modern, simplified Bent "Life Histories" volume. The numerous photos and their captions support and add to the text.

This book is not written for ornithologists. Although worth a browse, it cannot compete on an already crowded "science-books-to-buy" list. On the other hand, ornithologists should place it high on their list of appropriate gift items or references for amateur bird watchers and naturalists. It is a carefully crafted book that is quite successful at its intended level.—Peter F. Cannell.

Bird Conservation. 1 Edited by Stanley A. Temple. Univ. Wisconsin Press, Madison, 1983:vii + 148 pp. $12.95—The first number of a proposed annual publication sponsored

by the United States Section of The International Council for Bird Preservation is devoted primarily to a series of papers on raptors. The principal articles are: "Restoration of the Peregrine Falcon in the Eastern United States" by John H. Barclay and Tom J. Cade; "The Bald Eagle in the Northern United States" by James W. Grier et al.; "California Condor Reproduction, Past and Present" by Noel F. R. Snyder; and "The California Condor Recovery Program: An Overview" by John C. Ogden. There is a series of short papers on a variety of timely conservation matters, and a review of bird conservation literature listing 162 titles. This promises to be a very informative series filling an unoccupied niche.—GEORGE A. HALL.

NAME THAT DUCK. By Steven M. Cohen and Timothy Nowicki. Illus. by Timothy Nowicki. Name That Bird, 26349 Dundee Road, Huntington Woods, Michigan. 8 pp. field card, 108 black-and-white drawings. $1.95 + $0.25 postage.—The authors have devised a simple key for waterfowl identification based on the amount and location of white in the plumage. There is no text but the somewhat diagrammatic figures should enable the novice bird watcher or the sportsman to identify the ducks he sees on the water.—G.A.H.

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The Wilson Bulletin

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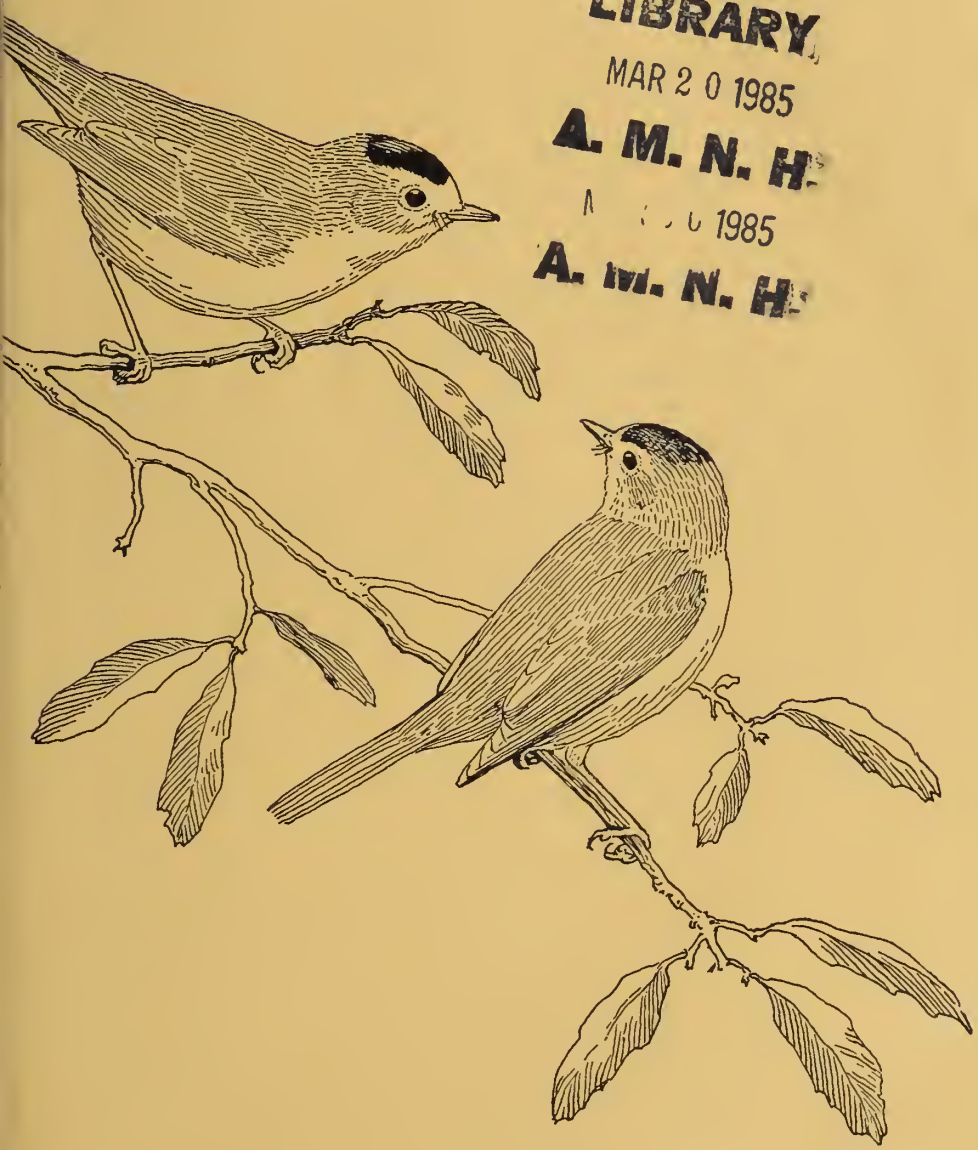

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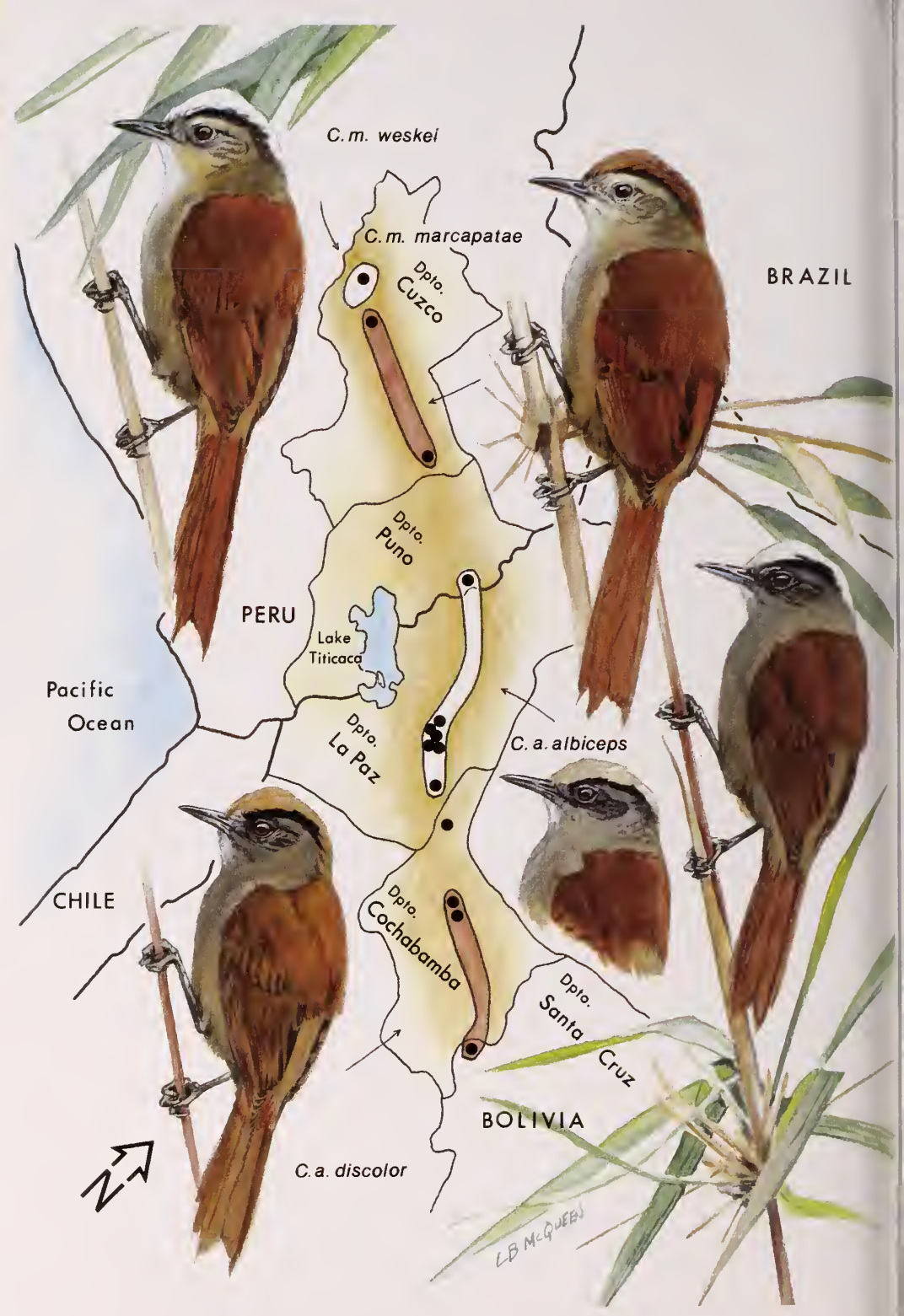

Cranioleuca albiceps and *C. marcapatae*, showing the development of rusty and white-crowned forms in each species and illustrating *C.m. weskei*, a new subspecies from the Cordillera Vilcabamba of south central Peru. From a watercolor painting by Lawrence B. McQueen.

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GEOGRAPHIC VARIATION, ZOOGEOGRAPHY, AND POSSIBLE RAPID EVOLUTION IN SOME *CRANIOLEUCA* SPINETAILS (FURNARIIDAE) OF THE ANDES

J. V. REMSEN, JR.

The humid slopes of the Andes Mountains of South America provide one of the world's greatest natural laboratories for the study of evolution and zoogeography. Although the "population structure," nature of geographic variation, and location of zoogeographic boundaries have been described for numerous taxa of the puna and paramo zones of the Andes (Vuilleumier 1980), relatively little has been published concerning birds of the humid, forested eastern slopes. In this paper, I analyze the geographic variation and distribution of the *Cranioleuca albiceps* superspecies (Furnariidae), here considered to consist of Light-crowned Spinetail (*C. albiceps*) (with two subspecies), Marcapata Spinetail (*C. marcapatae*), and a previously undescribed form, here considered a subspecies of *C. marcapatae,* to be called:

Cranioleuca marcapatae weskei subsp. nov.

HOLOTYPE.—American Museum of Natural History No. 820557; male from Cordillera Vilcabamba, elev. 3250 m, Dpto. Cuzco, Peru (12°36′S, 73°30′W), 22 July 1968; John S. Weske, original number 1825.

DIAGNOSIS.—Ventrally very similar to *Cranioleuca m. marcapatae,* but malar region more strongly washed buff; dorsally, virtually identical to white-crowned individuals of *Cranioleuca a. albiceps.*

DESCRIPTION OF HOLOTYPE.—Crown dull white, tinged buff on anteriormost forecrown; white of crown bordered laterally by black stripe that increases in width posteriorly; lores blackish mixed buffy white; eyebrow dull whitish above eye blending to Buffy Brown; faint, dull, blackish postocular line indistinctly delimits eyebrow; auriculars Olive-Brown with pale shaft streaks on some feathers; crown and black border blend raggedly into Saccardo's Umber neck and upper back; rest of back and upper wing coverts Chestnut; rump

and uppertail coverts Saccardo's Umber mixed with Chestnut; primaries Sooty Black except for outer web mainly Sanford's Brown; most secondaries Sooty Black except for Chestnut edge to outer webs and small Sanford's Brown apical spot; underwing coverts Olive-Brown mixed Cinnamon; rectrices Chestnut; outermost rectrices shortest and innermost longest and very pointed (typical *Cranioleuca* shape); chin and upper throat white, bordered laterally by poorly defined Warm Buff malar area; both throat and malar area blend gradually into darker lower throat, sides and chest, and belly, which are Light Grayish Olive to Light Drab; flanks, thighs, and undertail coverts Drab to Tawny. Bases of some feathers in vent area dull white. Soft parts in life: iris medium reddish-brown, maxilla black, mandible medium gray, tarsi and feet medium greenish-gray (black in dried specimen).

DISTRIBUTION.—Presently known only from cloud forest in the Cordillera Vilcabamba, Dpto. Cuzco, Peru, between 2620 and 3250 m.

SPECIMENS EXAMINED.—*C. m. weskei:* (AMNH) 3 ♂♂, 5 ♀♀, Cordillera Vilcabamba, Dpto. Cuzco, Peru, 12°36–37'S, 73°30–33'W, 2620–2640 m (3), 2830 m (1), 3250 m (3) and 3300 m (1). *C. m. marcapatae* (all Dpto. Cuzco, Peru): (LSUMZ) ♂, 14 km NE Abra Málaga on Ollantaitambo-Quillabamba road, 10,700 ft. (3210 m); (LSUMZ) ♂, ca 20 km NE Abra Málaga on Ollantaitambo-Quillabamba road, 9800 ft. (2940 m); (LSUMZ) ♂, ♀, San Luis on Ollantaitambo-Quillabamba road, 9000 ft. (2700 m); (LSUMZ) ♂, ♀, along Río Marcapata just below Marcapata on road to Quincemil, 9000 ft. (2700 m) (topotypes); (AMNH) ♀, Marcapata (topotype), *C. a. albiceps:* (LSUMZ) 2 ♂♂, 3 ♀♀, Valcón, 5 km NNW Quiaca, 3000 m, Dpto. Puno, Peru (first records for Peru); (LSUMZ) 8 ♂♂, 3 ♀♀, 1 sex ?, ca 1 km S Chuspipata, 3050 m, Dpto. La Paz, Bolivia; (LSUMZ) 5 ♂♂, 3 ♀♀, Cotapata, 4.5 km WNW Chuspipata, 3300 m, Dpto. La Paz; (ANSP) 3 ♂♂, 3 ♀♀, Hichuloma, 10,700 ft. (3210 m), Dpto. La Paz; (AMNH) 1 ♂, Rio Aceromarca, 10,800 ft. (3240 m), Dpto. La Paz. *C. a. albiceps* × *discolor:* (FMNH) 3 ♂♂, 1 ♀ (LSUMZ) 1 ♂, Choro, Prov. Ayopaya, Dpto. Cochabamba, Bolivia. *C. a. discolor:* (LSUMZ) 4 ♂♂, 1 ♀, 2 sex ?, (AMNH) 1 sex ?, km 104, 3100–3200 m, Prov. Chapare, Dpto. Cochabamba; (FMNH) 4 ♂♂, 4 ♀♀, (ANSP) 3 ♂♂, 2 ♀♀, (AMNH) 3 ♂♂, 1 ♀, (LSUMZ) 1 ♀, Incachaca 2400–2500 m, Prov. Chapare, Dpto. Cochabamba (topotype); (ANSP) 2 ♂♂, San Cristobal, 8500 ft. (2550 m), Dpto. Cochabamba; (FMNH) 2 ♂♂, 1 ♀, 28 km W Comarapa, Dpto. Santa Cruz, Bolivia (first records for Dpto. Santa Cruz).

REMARKS.—No differences in plumage pattern were detected between the sexes. Some slight variation among the eight specimens of *weskei* is apparent in grayness of the underparts and paleness of the superciliary; otherwise the series is very homogeneous in plumage and soft part colors. Vaurie (1980) previously identified the Vilcabamba specimens as *Cranioleuca albiceps* and published them as the first record for Peru.

ETYMOLOGY.—It is a pleasure to name this form for John S. Weske, preparator of the entire series from the Vilcabamba and co-leader of the several rigorous and highly productive expeditions to the area.

NATURAL HISTORY NOTES

All eight specimens of *C. m. weskei* were netted in elfin cloud forest along ridges. None of the specimens had the skull more than 20% pneumatized; as in numerous other synallaxines (pers. obs.), it seems likely that the skull never reaches complete pneumatization. Two of the three males had enlarged testes, but none of the five females was in reproductive condition; all were collected between 5 July and 8 August. None of the specimens had more than "little" fat, as is typical for funariids of the eastern slope of the Andes (pers. obs.).

Weske (1972) did not include information on *C. m. weskei* among the natural history data that he compiled for many Vilcabamba birds. It is likely that the natural history of this form is very similar to two relatives, *C. m. marcapatae* and *C. a. albiceps,* for which information is available. Parker and O'Neill (1980) found that *C. m. marcapatae* foraged in two's and three's in mixed-species flocks in bamboo thickets and mossy forest as did Remsen (in press) for *C. a. albiceps.* Both forms "hitch" along limbs to probe moss, bromeliads, dead leaf clusters, and bark; quantitative data on foraging behavior of *C. a. albiceps* are presented by Remsen and Parker (1984) and Remsen (in press). Contrary to Vaurie's (1980) implications from Niethammer's (1956) account, *C. albiceps* is very similar in foraging behavior to other *Cranioleuca* sensu strictu (see also F. Vuilleumier's note in Vaurie 1980:338).

Parker and O'Neill (1980) described the first known nest of *C. m. marcapatae.* On 1 August 1981, I found the first known nest of *C. albiceps*; it was under construction on a steep slope with dense undergrowth and patches of short trees at 3050 m near Chuspipata, Dpto. La Paz. The nest was an oval clump of moss, about 0.3 m in length, wrapped around the distal tip of a living bamboo (*Chusquea*) branch about 6 m above ground. The nest appeared virtually complete. The entrance was on the side about two-thirds of the way from the proximal to distal end (relative to the branch) of the nest; one bird was carrying moss into the nest chamber. Thus, this species' nest is very similar to that of *C. m. marcapatae.* Presumably the nest of *C. m. weskei* is similar.

RELATIONSHIPS AMONG THE TAXA

Should each of the four spinetail taxa in question be considered allospecies of a superspecies complex, subspecies of a single biological species, or some intermediate combination? In the absence of comparative data on vocalizations and other potential reproductive isolating mechanisms or on degree of genetic differentiation, any taxonomic decisions at this point for these primarily allopatric populations are tentative at best.

Current information indicates that crown color differences do not necessarily result in reproductive isolation. Specimens from an area (Choro, Prov. Ayopaya, Dpto. Cochabamba) geographically intermediate between populations of *C. a. albiceps* and *C. a. discolor* are intermediate in crown color between the white-crowned nominate subspecies and tawny-crowned *discolor.* Furthermore, the high frequency of buff-crowned individuals in the Dpto. La Paz population (see below) may indicate gene flow from the southern populations. Thus it seems best to disregard crown color, the character that varies most dramatically among populations, as a potential isolating mechanism (although this conclusion is based on the assumption

TABLE 1
PLUMAGE CHARACTERS IN THE *CRANIOLEUCA ALBICEPS* SUPERSPECIES

Taxon[1]	Plumage characters				
	Crown	Eyebrow	Auriculars	Throat	Breast
C. m. weskei	white	buffy-white	buffy-brown	white bordered buffy	gray-brown
C. m. marcapatae	chestnut	gray-white	gray-brown	white	gray-brown
C. a. albiceps	white or buffy	dark gray	dark gray	mostly gray-olive	olive-brown
C. a. discolor	tawny	dark gray	dark gray	mostly gray-olive	olive-brown

[1] Taxa are listed in geographic order from north to south.

that the populations in question are in secondary contact). Therefore, that *marcapatae* has a chestnut crown, in contrast to neighboring *weskei* and *albiceps,* in itself provides no evidence for reproductive isolation.

Except for crown color, *weskei* and *marcapatae* are much more similar to one another than either is to *albiceps* and *discolor.* Likewise, these latter two are virtually identical to each other except for crown color. Thus, on plumage characters other than crown color, the four taxa can be placed in two groups, the two paler northern forms, *weskei* and *marcapatae,* and the two southern forms, *albiceps* and *discolor* (Table 1).

To avoid changing currently recognized species limits in the absence of critical data, I recommend recognizing two species, *C. albiceps* (with two subspecies, the nominate form and *discolor*) and *C. marcapatae* (with two subspecies, the nominate form and *weskei*). Each of the two subspecies within each species is extremely similar in most plumage characters and differs from each other to about the same degree in crown color. This arrangement may seem unsatisfactory to some, because *C. m. weskei* and *C. a. albiceps* are virtually identical from the dorsal view. This resemblance, however, can be regarded as retention of a shared, primitive character, as proposed below.

Although reconstructions of historical zoogeographic events often contain more speculation than warranted by available data, such historical hypotheses are a necessary part of a zoogeographic and taxonomic analysis. Within the *Cranioleuca albiceps* superspecies, I assume that the white crown is a primitive character, because it seems unlikely that two isolated populations would have independently evolved an identical crown color that is unique in *Craniolecua* (and in the Furnariidae in general). Given this assumption, the following sequence of historical events is plausible.

Originally, a white-crowned population was distributed along the eastern slope of the Andes from the Cordillera Vilcabamba of Peru to Dpto. Cochabamba, Bolivia. Geological and climatological events isolated two populations from one another, proto-*marcapatae-weskei* north of and proto-*albiceps-discolor* south of some unknown barrier in southern Peru, perhaps the canyon of the Río Sangaban in northern Dpto. Puno. In isolation, the two populations differentiated in terms of plumage characters, mainly coloration of the underparts and face. Subsequently, the southern population was further fragmented by the dry canyon of the Río La Paz, and the population to the south of this barrier became tawny-crowned. Also, the northern population was divided in two by the dry canyon of the Río Urubamba, and the population to the south of the Urubamba became chestnut-crowned. These events would have led to the current pattern of distribution of the four forms, with *weskei* and nominate *albiceps* retaining the white crown, a shared primitive character (but a shared derived character for this species group as a whole). Study of other taxa from these regions are required to corroborate this pattern and document its validity (Nelson and Platnick 1981).

PATTERNS OF GEOGRAPHIC VARIATION IN COLOR AND SIZE

Geographic variation in body size in the *Cranioleuca albiceps* group shows the trend counter to Bergmann's "rule" but typical for birds of the humid southern Andes (Remsen 1981, 1982, unpubl.): decreasing size with increasing distance from the equator. Using wing length to index body size, there is a highly significant negative correlation between wing length and latitude: N (♂♂) = 31, $r = -.656$, $P < 0.001$; N (♀♀) = 24, $r = -.677$, $P < 0.001$. The trend is not a "perfect" one, however, because southernmost *discolor* averages slightly larger than nominate *albiceps* to the north.

At first glance, the *C. albiceps* superspecies seems to provide an example of a "leapfrog" pattern of geographic variation in color (Remsen 1984)—the two white-crowned populations are geographically separated from each other by a chestnut-crowned form. This example was not included in my list of taxa that show the leapfrog pattern because crown color is the only phenotypic character to show the pattern; the two northern forms, *weskei* and *marcapatae,* are much more similar to each other in all other plumage characters than either is to the two southern forms (Table 1). Those taxa included in the list showing the leapfrog pattern were those in which the majority of characters that showed geographic variation did so in a leapfrog manner.

Can an adaptive explanation be proposed for the different plumage types? I have previously suggested (Remsen 1984) that the leapfrog pattern

is best explained by invoking random change that is not environmentally induced. On the other hand, I have also observed (unpubl.) that in species in which degree of buffy, chestnut, or tawny (="rusty") coloration varies geographically, the "rustiest" form tends to occur at the southern end of the Andes, especially Dpto. Cochabamba, or to a more limited degree at the northern end of the Andes in extreme northern Colombia and Venezuela. Could this increased rustiness be an adaptation for better camouflage because longer dry seasons at the extremes of the Andes make the forest there have a "rustier" appearance? The rainfall data necessary for testing this hypothesis are not available.

POSSIBLE RAPID EVOLUTION IN CROWN COLOR

In 1980 and 1981, LSUMZ field parties collected 28 specimens of *C. a. albiceps* in Dpto. La Paz and 5 in Dpto. Puno. Variation in crown color in these recent specimens contrasts markedly with earlier descriptions, none of which indicated that crown color was anything but white. In contrast, the crowns of only four recent specimens were pure white; the rest were faintly to strongly washed with buffy. Because it seemed highly unlikely that earlier workers such as J. T. Zimmer and C. E. Hellmayr would have overlooked such variation, I began to investigate the possibility that a change in phenotype had occurred between 1936 and 1980.

First, I determined whether the crowns of the earlier specimens were indeed all white. As noted by Zimmer (1935), none of the earlier published descriptions of Dpto. La Paz birds (e.g., type description and Sclater 1980) indicated that the crown was any color other than white. I attempted to examine, or have others examine for me, all specimens of *Cranioleuca a. albiceps* available in museums. Four specimens collected before 1930, including the type specimen at the British Museum, have white crowns, with perhaps only some buffy tinge on forecrown. Five adults collected in 1934–35 also have white crowns, but two obvious juveniles have the crown noticeably tinged buff.

In contrast, specimens collected in 1980–81 show marked variation in crown color with over half of the specimens having their crowns strongly buffy or buffy mixed with white. This variation is not related to sex ($\chi^2 = 0.14$, df = 1, $P > 0.05$); 5 of 12 (42%) adult males and three of nine (33%) of adult females are buffy-crowned. Nor is the variation due to age. Because most individuals may never acquire a completely pneumatized skull (only 1 of 28 LSUMZ specimens with skull data is 100% pneumatized; most are labeled 5–25% ossified), analysis of the effect of age is difficult. Nevertheless, of the four specimens with traces of juvenile plumage, two are buffy-crowned and two are white.

TABLE 2

FREQUENCY OF CROWN COLOR TYPES IN OLD VS NEW SPECIMENS OF *CRANIOLEUCA A. ALBICEPS*

Specimen age	Number of specimens[1] in each crown color category	
	White	Buffy
1936	9	0
1977	9	15

[1] Only adults were included in the table; inclusion of birds in juvenal plumage would add two individuals to the "buffy" category for pre-1936 specimens, and two to the "white" category and two to the "buffy" category for post-1977 specimens.

That the difference in crown color frequencies in the pre-1936 specimens and the recent specimens could be due to geographic variation or anomalies in sampling appears improbable. The older collecting sites are located between the modern sites in Dpto. La Paz and Dpto. Puno, and Carriker's 1934–35 locality, Hichuloma, is only 2 km from, and on the same ridge as, the 1980–81 La Paz localities.

The proportion of individuals in the two crown color categories in old vs recent samples (Table 2) is significantly different ($\chi^2 = 5.9$, df = 1, $P < 0.05$) if juveniles are included and highly significantly different ($\chi^2 = 23.3$, df = 1, $P < 0.0001$) if only birds in adult plumage are analyzed. Two interpretations are possible. Conservatively, if the juveniles are included, one could argue that a combination of differences in sampling technique (guns for old specimens, mostly mist-nets for recent) and collecting localities produced a difference in proportions of borderline significance. On the other hand, especially if juveniles are excluded, one could argue, almost heretically, that a new phenotype is in the process of spreading through the population over a 40-year period. This possibility has also been suggested by Fitzpatrick (1980) for another Andean bird population—that of the White-winged Brush-Finch (*Atlapetes leucopterus*). In birds, such rapid evolutionary change has been reported so far only in species introduced into novel environments (Johnston and Selander 1964, Aldrich and Weske 1978, Baker and Moeed 1979, Barlow 1980), although Zink (1983) found minor changes in skeletal morphometrics in samples of a non-introduced bird population over a 50-year time span. In the case of *C. albiceps,* such change could be the result of: (1) introgression of *discolor* genes into the nominate *albiceps* population; (2) evolutionary change independent of secondary contact with *discolor* populations; or (3) change in frequency of a polymorphic character state. Available data do not allow evaluation of these alternatives.

SUMMARY

A distinct new form of *Cranioleuca* from the Cordillera Vilcabamba, Dpto. Cuzco, Peru, is described as a subspecies (*weskei*) of *Cranioleuca marcapatae*. Natural history notes concerning *weskei* and its close relative *C. a. albiceps* are presented, including a description of the first known nest of the latter. Relationships among the members of the *C. albiceps* superspecies are discussed, as are the patterns of geographic variation that this group exhibits in color and body size. Samples of *C. a. albiceps* taken approximately 50 years apart show strong differences in crown color frequencies that can be interpreted tentatively as a case of rapid evolution in a phenotypic character.

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Color Plate

Inclusion of the frontispiece of *Cranioleuca* spp. has been made possible through an endowment established by George Miksch Sutton (1896–1982). Painting by Lawrence B. McQueen.

Wilson Bull., 96(4), 1984, pp. 524–542

PHYSICAL DEVELOPMENT OF NESTLING BALD EAGLES WITH EMPHASIS ON THE TIMING OF GROWTH EVENTS

GARY R. BORTOLOTTI

Studies of avian growth have traditionally emphasized ontogenetic changes in body weight. However, the relative size and growth rate of different parts of the body have been useful in investigations of adaptive modifications of growth (e.g., O'Connor 1977, Ricklefs 1979a). In this paper I quantify the growth of flight feathers and various body components, and describe developmental changes in color and body contour feathers of Bald Eagles (*Haliaeetus leucocephalus*). Because growth rate is strongly associated with body size and mode of development (i.e., altricial or precocial) (Ricklefs 1968, 1973), the growth of Bald Eagles is of interest for it is North America's heaviest semi-altricial (Nice 1962) bird.

There is little quantitative information on the development of Bald Eagle nestlings. Very general descriptions of plumage changes, and some weight data, have been published for single (Stewart 1970, Gilbert et al. 1981) and a few (Herrick 1932) captive eagles. Bortolotti (1984a) presented growth data that can be used to determine the age and sex of wild Bald Eagle nestlings. Herein, I investigate the influence of sex on body size and feather growth, and how a chick's order in the hatching sequence within a brood may affect feather development. The timing of initiation of growth events will be a major consideration in assessing eagle development, as will both the absolute and relative growth rates. I also comment on parental nest attentiveness as it may relate to the thermoregulatory ability of the young.

METHODS

Data on the growth of nestling northern Bald Eagles (*H. l. alascanus*) were collected from 1980–1982 at Besnard Lake (55°20'N, 106°00'W) in north-central Saskatchewan. Details of fieldwork will be brief for they are also described in Bortolotti et al. (1983) and Bortolotti (1984a, b). The study area is described in Gerrard et al. (1983).

I monitored the development of 64 nestlings, most of which were of known age, from 48 nests. Fifty-one of these birds were examined throughout most of the 10–12-week nestling period. I always recorded weight, length of the culmen (without cere), and length of the middle toe (without talon) for each nestling. When the chicks were about 2 weeks old (or as soon as measurements were possible, e.g., flight feathers) I also measured the depth of the bill at the leading edge of the cere, width of the tarsus, and length of the tarsus, foot pad, hallux claw, wing chord, eighth primary and central rectrix. Only three measurements

were taken in the first 2 weeks because it was difficult or impossible to do otherwise given self-imposed time restrictions at the nest to limit the amount of disturbance to the birds. My method of measuring eagles is described in detail or diagramed in Bortolotti (1984a, c). Nestlings were handled an average of once every 6.7 days (usually every 5–8).

Because eaglets were not measured on day 0 (hatching) for all variables considered here, it was not possible to compare the average size of newly hatched chicks to their ultimate (asymptotic) size. However, data were available for a single bird. I collected an abandoned (naturally, not human-induced) egg which contained what appeared to be a fully developed embryo (Royal Ontario Museum 141311, in spirits) that would likely have hatched within a very short time. It closely resembles the embryo depicted in a photograph in Herrick (1932:432).

I graphically fitted individual growth curves (Ricklefs 1967) to data on weight and culmen length for 26 male and 21 female nestlings. I did not fit curves to data on each nestling for other variables either because the technique was not reliable given that early measurements were missing, or asymptotes were difficult to estimate. Instead, I applied the growth equations to the mean value per day of age for the depth of the bill, length and width of the tarsus, and length of the hallux claw and mid-toe for females. The analysis was only necessary for one sex because my purpose was to examine the relative growth of body components. To compare growth of body parts with different asymptotes, I calculated Ricklefs' (1967) growth index which replaces the time axis of the more usual growth curve. Growth is then expressed in units representing the time required to increase from 10–50% of the asymptote. Criteria for determining the sex of eaglets, and a comparison of nestling asymptotes to measurements of live mature Bald Eagles and study skins of eagles, are presented in Bortolotti (1984a).

I recorded the development of body plumage by noting the day the second down feathers emerged from the skin, and when feathers on various parts of the body first unsheathed and became noticeable. Because I did not inspect nestlings daily, feather development data were incomplete for some individuals. I also recorded the color of the eyes, skin, cere, culmen, gape, talons, and legs, but did not use a standard color chart.

I quantified the behaviors of nestlings and adults from tree-top and ground blinds situated near nests. Behavioral data presented here were based on 1131 h of observation of nine nesting attempts, three per year, from 1980–1982 (see Bortolotti 1982, 1984b; Bortolotti et al. 1983 for details).

RESULTS

Color.—On the day of hatching, eaglets had dark brown eyes, the gape and legs were pink, and the skin was bright pink. The cere was very pale gray and the culmen was dark gray-black with a white tip. The talons were largely flesh colored. By day 1 the skin had faded to a soft pink, and the legs faded to a flesh tone. Beginning on day 2 and 3, but more usually on day 4 or 5, the skin became tinged with blue. Between day 4–8 the skin turned from largely pink to largely blue except for a small area under the wings. When the eaglets were 4–8 days old, the cere was pale yellow, the bill was dark gray-black, and the legs were pink-yellow. From 9–12 days the cere was pale olive, and the legs were pale yellow with some areas still pink-yellow. When 13–17 days old the legs were pale yellow, the cere was medium gray, and the culmen was very dark gray-black. The

TABLE 1
PARAMETERS OF GOMPERTZ EQUATIONS FOR WEIGHT AND CULMEN LENGTH GROWTH OF BALD EAGLES

Variable	Sex	N	Growth parameter		
			K $\bar{x} \pm$ SD (range)	t $\bar{x} \pm$ SD (range)	a $\bar{x} \pm$ SD (range)
Weight	M	26	0.0683 ± 0.00330 (0.063–0.077)	20.85** ± 1.153 (18.2–22.8)	4066*** ± 178.9 (3575–4500)
	F	21	0.0683 ± 0.00403 (0.057–0.075)	21.80 ± 1.297 (19.2–24.9)	5172 ± 213.3 (4800–5600)
Culmen length	M	26	0.0553 ± 0.00414 (0.047–0.062)	6.97*** ± 0.972 (5.2–8.8)	49.14*** ± 1.315 (45.5–51.0)
	F	21	0.0538 ± 0.00506 (0.045–0.062)	8.78 ± 1.325 (5.6–12.1)	54.39 ± 1.074 (52.0–56.5)

** Males are significantly different from females, ANOVA $P < 0.01$.
*** Males are significantly different from females, ANOVA $P < 0.001$.

talons darkened and became grayish at the junction of the phalanges and were light brown distally. Colors intensified during the 18–22 day period; the legs became a deeper yellow, the cere was medium-dark gray, and the bill, especially the lower mandible, was still darkening. The talons were blackish with a brown tip. I recorded no further color changes except an intensifying of colors in certain areas (e.g., legs).

Weight.—The relationship between egg weight and hatching weight for chicks has not been documented for Bald Eagles. For one egg artificially incubated by Gilbert et al. (1981), the chick weighed about 76% of the weight of the egg just prior to hatching. In my study one eaglet upon hatching weighed 71% (85 g) of the weight of its egg measured 2 days before. The average weight of Besnard Lake nestlings (91.5 g, SD = ±5.17, N = 6) measured on day 0 (but not necessarily at the time of hatching) was 79.9% of the weight of the average fertile egg (114.4 g, SD = ±10.59, N = 17) near the time of hatching. This is comparable to the results of Olendorff (1974) for Red-tailed Hawks (*Buteo jamaicensis*) (78.6%) and Ferruginous Hawks (*B. regalis*) (77.3%).

Table 1 presents data for the Gompertz growth equation parameters K (a constant proportional to the overall growth rate), t (the inflection point), and a (the asymptote) for weight curves. The asymptotes were not correlated with the K or t values of either sex (Ps > 0.05). However, K and t were highly significantly correlated for males ($r = -0.773$, df = 24, $P < 0.01$) and females ($r = -0.635$, df = 19, $P < 0.01$). Males were significantly smaller and had earlier inflection points than females, but were no

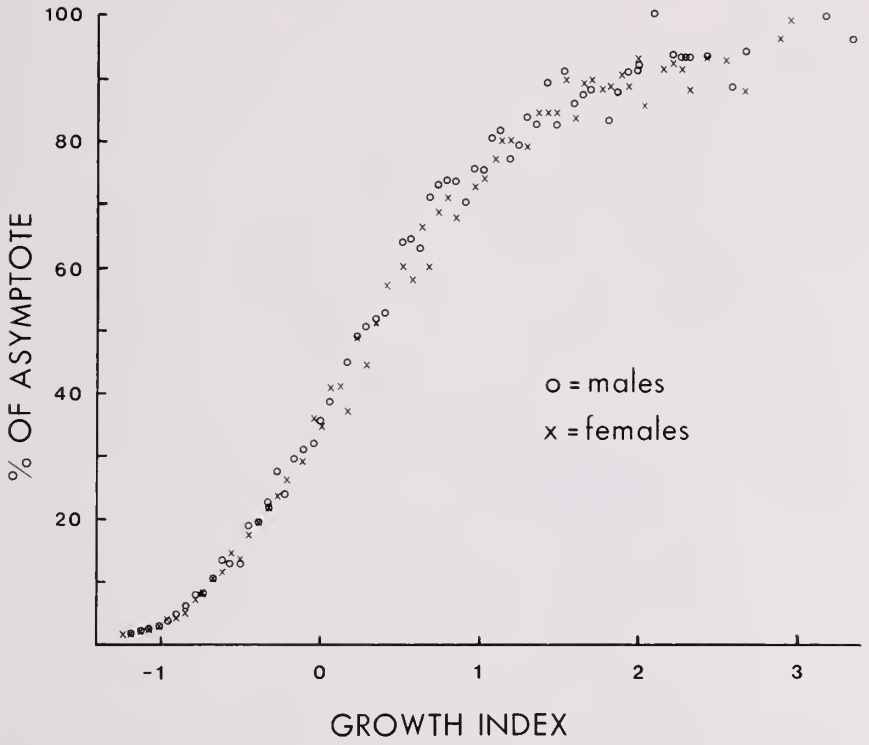

FIG. 1. The relative weight growth (percent of asymptote attained in relation to the growth index) for male (o), and female (x), nestling Bald Eagles. Points represent the mean weight for each day of age.

different in growth rate. However, when the average weight curves of the sexes were compared using the growth index, the relative growth of males and females was the same (Fig. 1).

Because of the Bald Eagle's large body size, daily weight gain can be substantial (up to 180 g/day, Fig. 2). The maximum rates shown in Fig. 2 are artificially lowered somewhat by the fact that each point represents the average gain over the 5–8 days between successive measurements. The absolute growth rate (dW/dt) for the Gompertz equation can be calculated by the formula:

$$dW/dt = -KaW(\log_e W)$$

where K is the growth rate constant, a is the asymptote, and W is the fraction of the asymptote of the growth curve attained (Ricklefs 1967, 1968). At the inflection point of the growth curve ($W = 0.37$), when

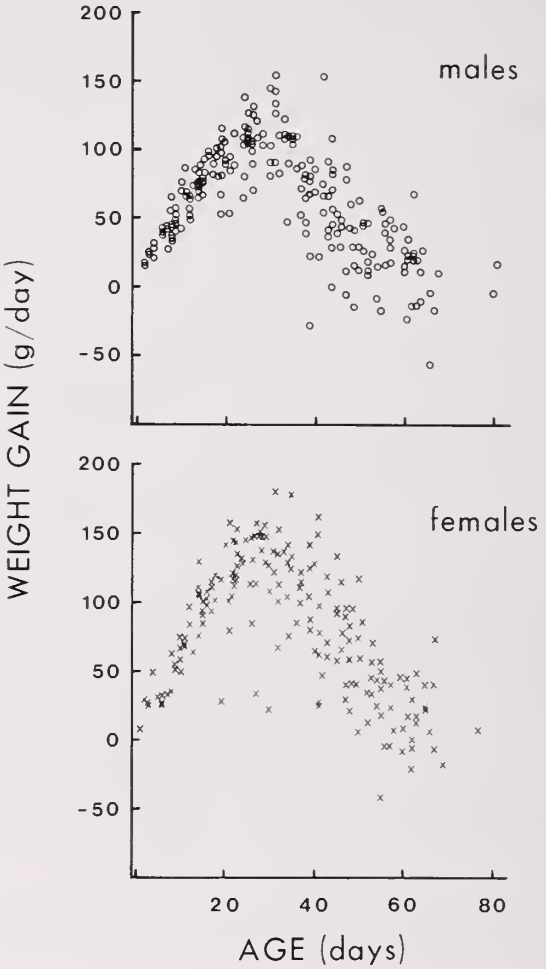

FIG. 2. Weight gain (g/day) as a function of age for male and female nestling Bald Eagles. Each point represents a single measurement.

maximum growth occurs, the average male and female Bald Eagle (Table 1) should gain weight at a rate of 102 and 130 g/day, respectively. The weight gain per day expressed as a percent of the total body weight on that day is illustrated in Fig. 3. The largest relative weight gains were early in the nestling period.

Body components.—Table 2 presents the absolute and relative size of an embryo near hatching. The body cavity is small, but the bill and legs are relatively large. This chick was small compared to most hatchlings.

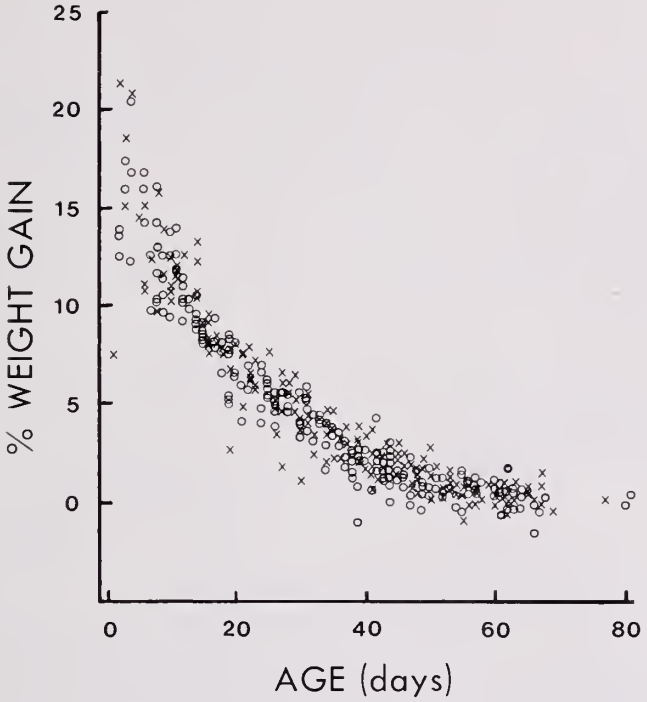

FIG. 3. Weight gain per day as a percent of body weight on that day, as a function of age for male (o), and female (x), nestling Bald Eagles. Each point represents a single measurement.

The volume of its egg (100.8 ml, calculated from the equation in Stickel et al. 1973) was only 86% of the mean volume (116.95 ml, SD = ±12.010, N = 18) for all other eggs I examined. However, as it is the relative size of the body components that is of interest in this paper, absolute size and sex of this eaglet are inconsequential.

The average value for the various body measurements per day of age for males and females is illustrated in Fig. 4. While the sexes were initially the same size, sexual dimorphism began to appear in some variables after 20 days of age (also see Bortolotti 1984a). As shown in Table 1, the parameters of the Gompertz equation for culmen length growth exhibited the same differences between the sexes as those of weight.

The relative growth of the body components is shown in Fig. 5. The length and width of the tarsus and length of the mid-toe reached asymptotic size at about the halfway point in the nestling period (Fig. 4). These three variables were characterized by a logistic growth curve. The hallux

TABLE 2
SIZE OF A BALD EAGLE NEAR HATCHING AGE

Variable	Absolute size[a]	Relative size (% of asymptotic size)[b]
Bill depth[c]	9.0	26
Culmen length[d]	10.7	21
Tarsus width[d]	2.9	19
Tarsus length[d]	9.1	13
Mid-toe length[d]	8.9	13
Hallux claw length[c]	4.1	10
Foot pad length[d]	16	6
Weight[d]	73[e]	2

[a] Linear measurements in mm, weight in g.
[b] Mean size of the sexes.
[c] See Bortolotti (1984c) for asymptotic size.
[d] See Bortolotti (1984a) for asymptotic size.
[e] Estimate based on the relationship between egg volume and egg weight (Bortolotti, unpubl.).

claw, culmen length, and bill depth conformed to the Gompertz equation and were still growing when the birds left the nest.

Flight feathers.—When the length of the eighth primary was used in a linear regression as a predictor of age, the confidence limits about individual predictions were about ±3 days, with similar results for central rectrix length (Bortolotti 1984a). To test for sexual differences in development, I randomly selected a subset of data whereby males and females were represented by equal numbers of first-hatched (C1) and second-hatched (C2) nestlings to avoid any bias that hatching sequence may introduce. This data set was comprised of 78 measurements of males and 72 measurments of females for both eighth primary and central rectrix. The emergence of the eighth primary (i.e., the intercept of the regression equation) was significantly earlier for males than for females ($F = 15.84$, $df = 1,147$, $P < 0.0001$). The same pattern was true for the emergence of the central rectrix ($F = 18.07$, $df = 1,147$, $P < 0.0001$). There was no statistical difference ($Ps > 0.05$) between the sexes in the slope of the regressions (i.e., the rate of growth) for either the primary feather or the rectrix.

For neither sex was the growth of flight feathers complete at the time of nest departure, as apparently is the case for several raptors (Brown and Amadon 1968). Young eagles frequently leave the nest before they can fly and have to spend a few days on the ground (pers. obs.). I captured 20 eaglets that had "prematurely" left the nest, and sheaths of growing flight feathers were evident on all of them. The asymptotic size of the flight features was not known. If, however, the lengths of the eighth pri-

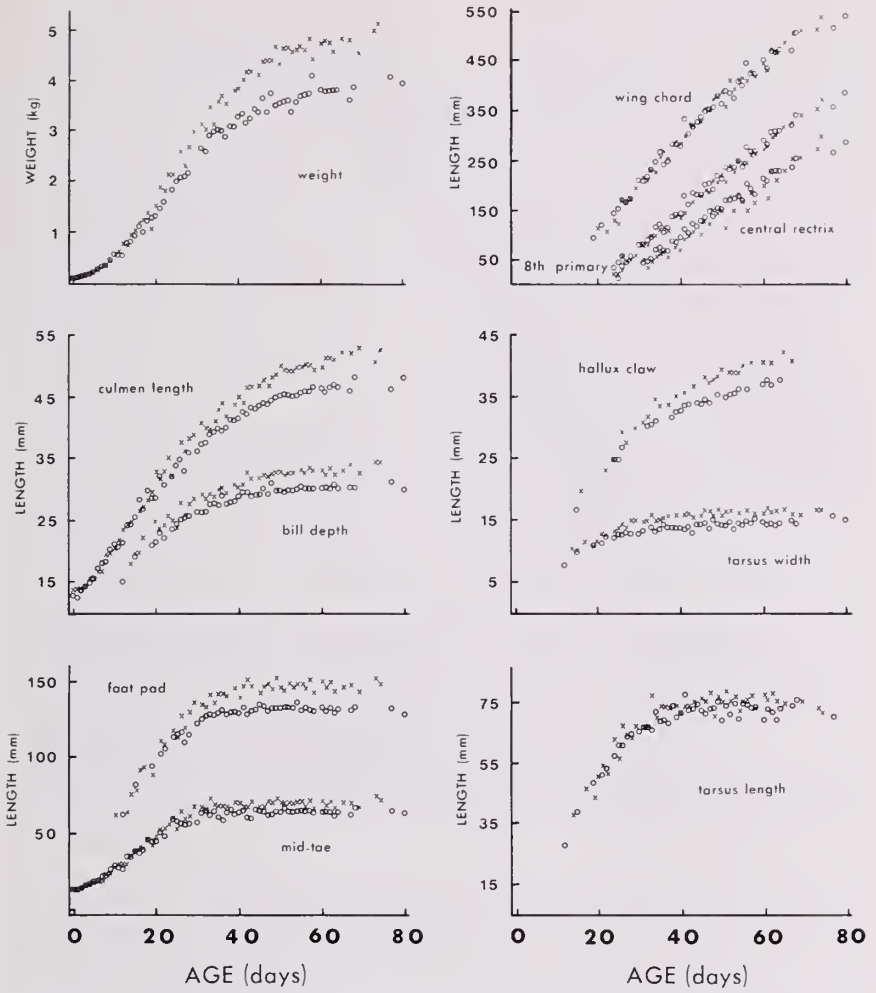

FIG. 4. Mean size as a function of age for body measurements of male (o), and female (x), nestling Bald Eagles.

mary, wing chord, and central rectrix of study skins (youngest plumage class of Bortolotti 1984c) are comparable to the asymptotes of these characters for nestlings, then measurements made on the captured birds reveal that only 80%, 88%, and 84%, respectively, of growth was completed. Eaglets on the ground were usually airborne within a day or two and it is unlikely that feather growth could have been completed in that time. Because flight feathers were not fully grown until after nest departure,

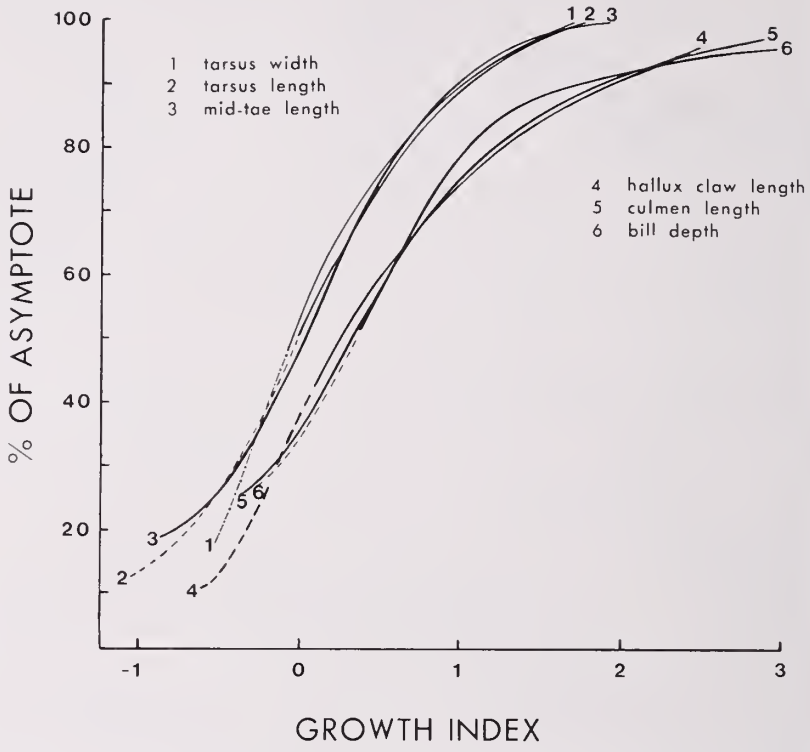

FIG. 5. The relative growth (percent of asymptote attained in relation to the growth index) for culmen length, bill depth, hallux claw length, mid-toe length, and the length and width of the tarsus (for females only, see text).

and because of the earlier feather development of males, sexual size dimorphism was not apparent in the measurements of wing chord, eighth primary, and central rectrix made during the nestling period (Fig. 4). The mature sizes of these variables are, however, significantly sexually dimorphic (Bortolotti 1984c).

To examine the potential effect that order in the hatching sequence may have had on flight feather growth, I compared C1s to C2s within each sex. For eighth primary length, the slopes of regressions were not statistically significantly different (Ps > 0.05) for either sex, but the intercepts were significantly different for males ($F = 4.74$, df = 1,99, $P = 0.03$) and females ($F = 30.04$, df = 1,92, $P < 0.0001$). The rate of central rectrix growth also did not differ between chicks (Ps > 0.05), but the timing of the intercept did for males ($F = 4.95$, df = 1,99, $P = 0.028$) and females

($F = 16.14$, df = 1,92, $P = 0.0001$). The emergence of both feathers was delayed for C2 compared to C1.

For a more detailed investigation of factors influencing flight feather growth, I calculated a linear regression equation for the relationship between age and the length of the eighth primary for each nestling for the linear period of feather growth (up to 72 days of age, Bortolotti 1984a). This allowed comparison of both the growth rate and time of emergence of the primaries to the weight growth parameters K and t. The growth rate constants K were not significantly correlated with the slopes of the eighth primary regressions ($P > 0.05$), but were correlated with the intercepts for males ($r = -0.518$, df = 24, $P < 0.01$) and females ($r = -0.457$, df = 19, $P < 0.05$). These results are consistent with those of the previous investigation of the relationship of primary feather growth to sex and order in the hatching sequence; the timing of emergence of the feather, but not growth rate, was important. The intercepts of the eighth primary regressions were also significantly correlated with the inflection points of the weight growth curves for males ($r = 0.655$, df = 24, $P < 0.01$) and females ($r = 0.607$, df = 19, $P < 0.01$).

Body feathers.—Fig. 6 shows the general appearance of nestlings of various ages. Upon hatching, eaglets were covered with a light beige-gray prepennae down (Fig. 6A). The color was more or less uniform over the body. Bent (1937) described the first down of the southern Bald Eagle (*H. l. leucocephalus*) as smoke-gray on the back, paler gray on the head and underparts, and nearly white on the throat.

The first down was gradually replaced by a noticeably darker medium gray second (preplumulae) down. The second down began to appear through the skin between 9 and 11 days of age (Fig. 6B). No sex difference was noted in the timing of the growth of the second down, but there was an effect for the order with which nestlings hatched within a nest. In broods of two chicks, emergence of second down of the second-hatched chick (C2) was delayed by about 1 day compared to the first-hatched chick (C1) (Sign test, N = 9, $P = 0.02$). The retarded development of C2 is evident in Fig. 6C. Although the siblings in Fig. 6C were only 1 day different in age, their plumage would suggest a greater disparity. By 18–22 days of age very little first down was visible on the body except for the top of the head, where second down was beginning to show (Fig. 6D).

The first contour feathers to show on the body were those of the humeral tract, appearing as dark epaulets (Fig. 6E). These first became evident on day 24–31. Feathers on the head and upper back first appeared on day 25 at the earliest and day 34 at the latest (Fig. 6F). Feathers on the lateral ventral surface became noticeable between day 26 and 45 (Fig. 6G), and

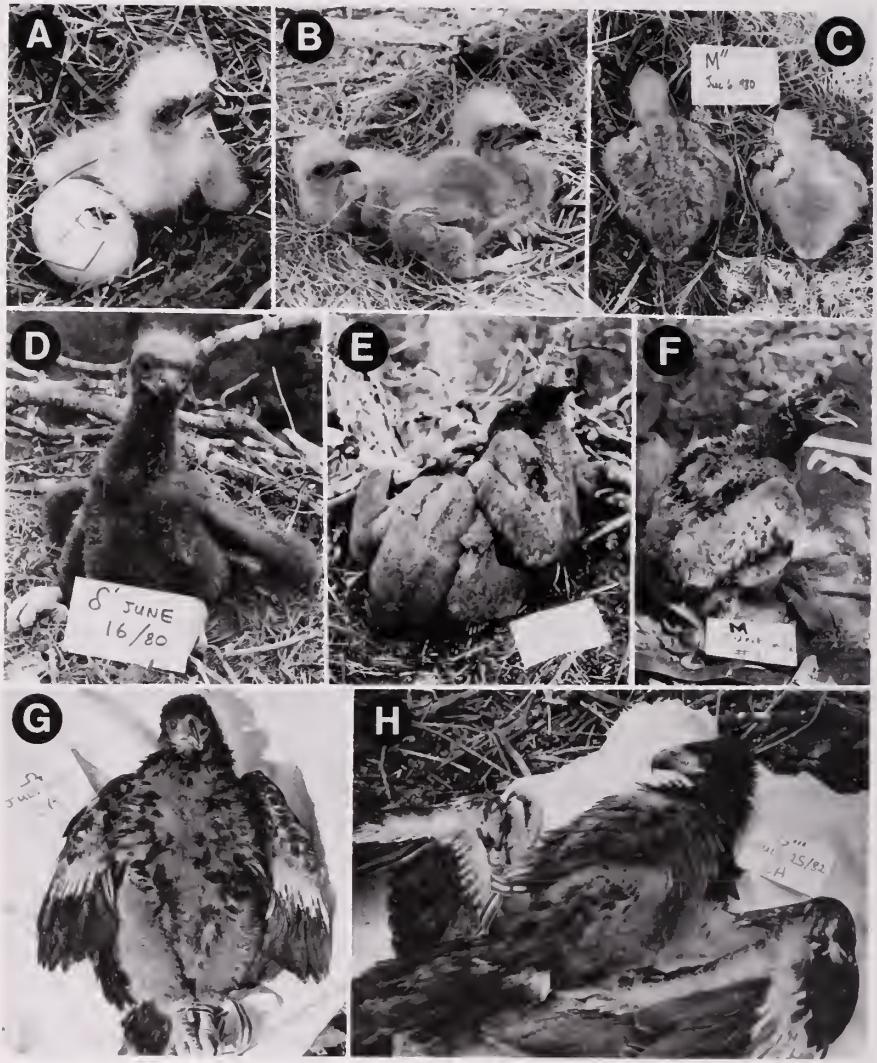

FIG. 6. Physical appearance of Bald Eagle nestlings of different ages (actual age and an approximate range of possible ages for a bird of that degree of development): (A) 2 days (1–5); (B) left = 8 days (6–9), right = 10 days (10–13); (C) left = 13 days (12–16), right = 12 (9–12); (D) 19 days (18–23); (E) left = 24 days (19–23), right = 26 days (24–31); (F) 28 days (27–35); (G) 44 days (32–48); (H) 56 days (50–65). The white card shown in some photographs was 7.6 × 12.7 cm in size.

those covering the tarsi were last to show between 39 and 55 days of age (Fig. 6H).

There was no indication of a sex difference in the timing of appearance of body feathers. However, this would have been very difficult to detect given the large variance associated with the age of appearance of feathers for most parts of the body, particularly those developing late in the nestling period. Collopy (1980) found no difference in the rate of development of six of eight feather tracts of nestling Golden Eagles (*Aquila chrysaetos*). According to Newton (1978), male Sparrowhawks (*Accipiter nisus*) appeared to have more advanced plumage than females.

It was strikingly obvious to me in the field that two eaglets of the same age could look very different because of the variability in timing of emergence of body feathers. To investigate the degree to which differences in body feather maturation were correlated with other developmental processes, I classified the birds as being either early or late. The criteria for early developers were: the age of appearance of feathers had to be less than or equal to 26 for the humeral tract, 30 for head and back feathers, and 43 for tarsal feathers. My field notes were detailed enough to determine the timing of feather growth for 19 early and 14 late developers. I used Mann-Whitney *U*-tests to compare early and late classes. There were no significant differences (Ps > 0.05) for Ks (sexes combined), ts (sexes tested separately), and as (sexes tested separately) of the weight growth curves. The slopes of the individual eighth primary regressions were not different between groups ($P > 0.05$). There was also no difference for eighth primary intecepts for males ($P > 0.05$), but there was a significant difference for females ($P < 0.01$). Although there was little or no association between body feather development and weight and primary feather growth, the early and late categories do seem to be good indicators of development; there was a significant difference in the age at which males ($P < 0.01$) and females ($P < 0.01$) departed from the nest. Early developing males left an average of 4.8 days younger than late developing males. Early developing females left an average of 4.7 days younger than late developing females.

Homeothermy.—I did not empirically determine the age at which nestlings began to thermoregulate. Dunn (1975) found that growth rate (K) was a good predictor of the age at which altricial birds became homeothermic. If Bald Eagles are comparable to the species Dunn (1975) examined, then eaglets should have begun to thermoregulate at 14.7 days of age (K was first converted to the logistic equation equivalent [Ricklefs 1973]). If the interspecific relationship of K and age of homeothermy derived by Dunn (1975) also applies intraspecifically, then the range of

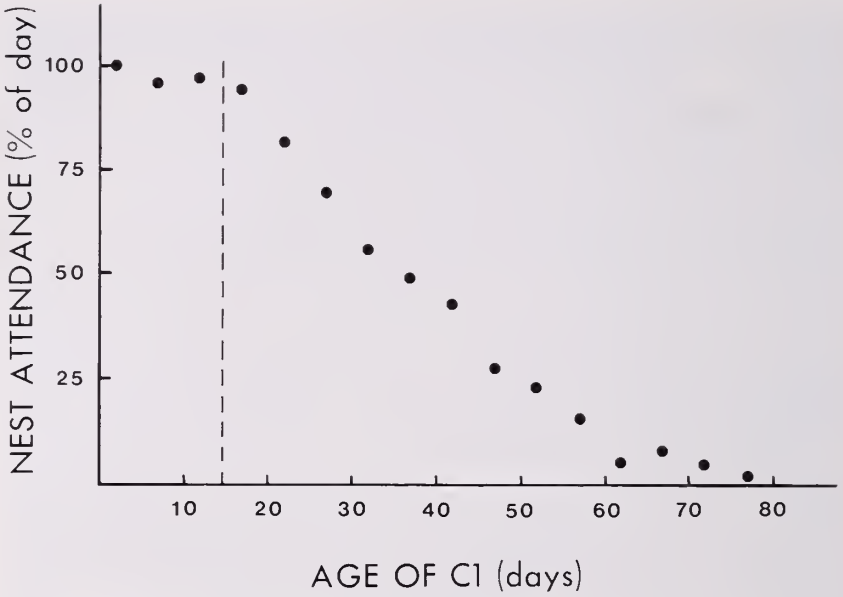

FIG. 7. Percent of time at least one adult Bald Eagle was in attendance at the nest as a function of the age of the first-hatched chick (C1). Points represent the mean for 5-day periods, plotted mid-way into each period. The dashed line marks the estimated age at which eaglets began to thermoregulate.

ages for eaglets was 14.5–15.1 days. Most species of altricial birds brood their offspring for a large portion of the day until the chicks begin to thermoregulate. As the ability of the nestlings to control their own temperature improves, the adults should be free to spend increasing amounts of time away from the nest foraging (Dunn 1975). This may be true for Bald Eagles, for the estimated age of homeothermy coincides with a sharp decline in the amount of time at least one adult is present at the nest (Fig. 7).

DISCUSSION

Feather development.—Little is known about the functional significance and implications of different patterns of feather growth (Ricklefs 1983). The development of Bald Eagles is typical of other falconiforms; wing and tail quills are first to emerge, and then the body feathers with those on the upper side being earliest (Brown and Amadon 1968).

Plumage development is associated with the acquisition of homeothermy (Ricklefs 1983). At the time when eaglets were estimated to become homeothermic, feather development was restricted to an increase

in the proportion of second down. The second down is much thicker than the first (Herrick 1932, Bent 1937, pers. obs.), and thus presumably has better insulative properties. Given that the emergence of second down is delayed in C2 eaglets, C1 nestlings may be able to achieve "effective," if not "physiological" (see Dunn 1975), thermoregulation at a younger age than C2s.

Hatching order within a brood also had an effect on the timing of emergence of the eighth primary and central rectrix. Although not quantified in this study, body contour feather development appeared to be delayed as well. Examples of how much the feather development of C2 chicks can be hindered by the presence of an older sibling can be seen in photographs of White-tailed Eagles (*H. albicilla*) in Mori (1980), and of Booted Eagles (*Hieraaetus pennatus*) in Steyn (1983). A comparison of the appearance of the siblings in these two examples would suggest an age disparity between them far in excess of the actual difference. Undoubtedly, the same phenomenon led Broley (1947) to believe that Bald Eagle eggs could be laid 2–3 weeks apart because of the apparent age difference of chicks within a nest (eggs usually hatch 1–3 days apart [Bortolotti 1984b]).

The development of body feathers was not associated with any parameters of the weight growth curves. This is likely because most of the body feathers began to emerge relatively late in the nestling period. Eaglets reached approximately 45% of asymptotic weight when the first contour feathers appeared, and 75% when the legs began to feather out. Feather growth may have been influenced by short-term effects, e.g., a variable food supply, that were of little consequence to weight gain at that particular stage of development. Body feather growth also appeared to be independent of growth rate of the eighth primary and perhaps its timing of emergence as well.

Unlike body feathers, aspects of eighth primary growth were associated with weight growth parameters. The appearance of the feather was significantly correlated with K and t of the weight growth curves. The eighth primary emerged from the wing at about the time of maximum weight gain (i.e., the inflection point of the weight growth curve) and thus both weight and feather growth may have been influenced by the same environmental and physiological conditions. I did not find any significant relationships to explain the variation in the rate of eighth primary growth. Ricklefs (1984) found that the more rapid the weight growth of European Starlings (*Sturnus vulgaris*), the earlier the primary feathers began to grow, but the rate of feather elongation was not affected. Several researchers studying raptors have found that flight feathers show relatively little variance in growth rate and are less likely to be influenced by food shortages than weight growth (Scharf and Balfour 1971, Moss 1979, Picozzi 1980,

Olsen et al. 1982). In contrast, Zach and Mayoh (1982) found that the flight feather growth of Tree Swallows (*Tachycineta bicolor*) was more variable than weight growth. While the appearance of the feathers of swallows with long nestlings periods was delayed, there was no relationship between the timing of feather growth and weight growth.

Flight feather growth varies little among individuals compared to body feather development. This suggests a high priority of functional importance for flight feathers (O'Connor 1977). The relative independence of body and flight feather growth may allow for energy and nutrients to be restricted to areas of relatively great importance to post-fledging survival. If this is true, the detriment of food shortages to the growing young is minimized. This is not to say that body feather development is unimportant, for it may be indicative of other developmental processes of the body. This is suggested by the fact that "early" birds left the nest nearly 5 days sooner that "late" birds. Body feather development may thus be a useful means of monitoring environmental stress in this species.

Body size.—Interspecifically, growth rate is inversely related to body size in birds (Ricklefs 1968). Such is not the case intraspecifically; rapid growth of eaglets was associated with early inflection points of growth curves, but neither of these attributes were related to the asymptotic weight. The Bald Eagle grows at a rate expected of an altricial bird of its size. Ricklefs' (1968) model of growth rate and body weight for temperate zone passerines and raptors predicts a rate (using t_{10-90}, an inverse measure of growth) of 41.2 days, whereas the observed was 45.1. Because eagles are large and have a semi-altricial mode of development, absolute growth rate should be substantial. In fact, the Bald Eagle may gain more weight per day than any other North American bird. I have not found any reference to species exceeding the maximum weight gain of 180 g/day (a conservative figure, see Results) reported here.

Several hypotheses have been proposed to account for species-characteristic growth rates in birds. They are reviewed in Ricklefs (1983) and tested for eagles in Bortolotti (1984b) and so will not be discussed in detail here. I will, however, comment on the relevance of data presented here to aspects of the topic.

Ricklefs (1973, 1979a, 1979b) proposed that the rate of growth of any body component is constrained by a compromise between allocation of tissue to embryonic and mature functions. The more mature the tissue is, the slower its growth rate will be. Consistent with this hypothesis is the slow growth of the Bald Eagle's bill. The bill is not only functional in feeding, as eaglets must initially take food from their parents' bills (they do not gape) and then later tear up prey themselves, but it is also important in sibling conflicts. Very young eaglets are capable of forceful bites and

pecks, and of shaking a sibling from side to side. Eaglets also begin preening soon after hatching, which may be important in reducing parasite loads (Bortolotti 1985). Of course, the bill is not the only body component associated with performing these behaviors, and perhaps the maturation of jaw muscles is the more important consideration. Seemingly inconsistent with the tissue-allocation hypothesis is the slow growth of the hallux claw which has a low degree of functional maturity in the nestling period. Perhaps the growth of the bill and claw are slow partly because of their horny exteriors. The hard sheath covering the bone may not be capable of more rapid elongation and thus limits growth.

A comparison of growth rates of various parts of the body, within and among species, led Ricklefs (1979a) to believe that the overall growth rate of an individual was limited by the most slowly growing component. The slow growth of the bill (and presumably head) probably does not limit the overall rate to any great degree because a large proportion of bill growth was achieved prenatally (Table 2), thus allowing for faster growth postnatally (Ricklefs 1979a).

CONCLUSIONS

It is tempting to hypothesize scenarios of adaptive significance to explain variation in growth rates (O'Connor 1977, 1978; Werschkul 1979). However, it is difficult, if not impossible in most cases, to attribute the patterns of growth directly to natural selection acting on growth itself. Alternative explanations are possible such that the observed growth rate is merely the consequence of selection operating on other factors (Ricklefs 1983).

Several studies of the growth of birds that are sexually dimorphic in size have documented a similar pattern of development of the sexes (see review by Richter 1983). The smaller sex is characterized by earlier development of feathers, faster attainment of asymptotic size, and earlier flights from the nest. That this is true regardless of whether males or females are the larger sex suggests that biochemical processes in growth likely proceed at a specific rate and sex-related differences are the allometric consequence of size dimorphism. When the difference in size is accounted for, males and females grow at the same rate (Fig. 1). While sexual dimorphism in growth dynamics may have several important consequences for nestling survival (Newton 1978, Bortolotti 1984b), and sex ratio (Richter 1983, Bortolotti 1984b), the rate of growth is unlikely to have been the primary adaptation in such cases.

Results of this study consistently showed that the timing of growth events, whether in regard to sex differences or the effect of hatching sequence, was a more important consideration than rate of growth in as-

sessing development. Growth studies have traditionally lacked emphasis on the timing of growth events compared to the concern for the rate at which growth proceeds. This may be in part because of the mathematical ease of comparing K values among species characterized by different growth equations (Ricklefs 1968, 1973). Studies of intraspecific variation are not so limited, and researchers should strive to document as many facets of growth as possible.

SUMMARY

Developmental changes in color, weight, body size, and the appearance of body contour feathers, are described for wild nestling Bald Eagles (*Haliaeetus leucocephalus*) in Saskatchewan. Chicks hatched with relatively large bills, large legs, and a small body. The growth of some body components (e.g., the legs) was complete about halfway through the nestling period, whereas the mature size of the bill and flight feathers was not reached until after the birds left the nest. The maximum absolute weight gain per day (180 g, a conservative figure) of Bald Eagles appears to be the greatest of any North American bird, but this is to be expected of a temperate zone altricial species of its body size. Weight growth was not correlated with body feather development or the rate of eighth primary feather growth, but was significantly correlated with the timing of the emergence of the eighth primary. There was a great deal of variation in the age at which body feathers unsheathed, yet little variation in the growth of flight feathers. Body feather growth and primary feather growth were largely independent. Males differed from females in being smaller, having earlier inflection points to growth curves and growing flight feathers at a younger age, but were not different in rate of growth. When body size was accounted for, the relative growth of the sexes was equal. The emergence of second down and flight feathers was delayed for the second-hatched chick in the nest compared to its older sibling. The age at which eaglets became homeothermic was estimated to be about 15 days, at which time a sharp decline in the nest attentiveness behavior of the parents was observed. Caution must be exercised when attempting to determine the adaptive significance of patterns of growth, for growth itself may not have been the primary adaptation. Several analyses presented here showed that the timing of growth events, rather than the rate at which they proceed, was the more important consideration in assessing development.

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CHANGE IN EDITOR

Dr. Keith L. Bildstein will be serving as the Editor of The Wilson Bulletin beginning with Volume 97. As of 15 May 1984, all manuscripts submitted for publication in the journal should be sent to him at the **Department of Biology, Winthrop College, Rock Hill, SC 29733.** All manuscripts received prior to 15 May 1984 will continue to be processed by Dr. Jon C. Barlow.

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SUGGESTED TECHNIQUES FOR MODERN AVIAN SYSTEMATICS

Ned K. Johnson, Robert M. Zink, George F. Barrowclough, and Jill A. Marten

The methodology of avian systematics at the population and near-species levels has changed profoundly in recent years. Increasingly, we see the application of quantitative analytical approaches, such as audiospectrography, reflectance spectrophotometry, multivariate morphometrics, and pigment and tissue biochemistry. However, gel electrophoresis and the histochemical staining of tissue, techniques that reveal genetic loci encoding specific proteins, have only recently been extensively used on avian material (Barrowclough 1983, Corbin 1983). Because so few studies have been conducted, there has been insufficient time and experience for a consensus to develop as to which technical procedures are most appropriate for birds. Although laboratory protocols for the electrophoretic analysis of vertebrate tissues are in general well established (Yang 1971), the literature lacks detailed information of use to the field worker on the sampling, preservation, and transport of avian tissue for electrophoretic work. Furthermore, there are possible shortcuts in laboratory procedures and experimental design that may not be widely appreciated. The present paper attempts to fill these gaps.

The advent of multidimensional and multiple character set approaches in avian systematics has also revealed certain shortcomings in standard techniques of specimen preparation. Although traditional methods of preparing skins and skeletons (Hall 1962:26–35) continue to be acceptable for many purposes, unorthodox kinds of preparations often are better suited for studies examining specific issues in modern speciation-variation research. An example of such an issue is mosaic evolution, the phenomenon of differential rates of change in different character suites (Dobzhansky et al. 1977:31). For several reasons, birds are unusually well suited for the examination of mosaic evolution. For example, avian vocalizations and plumage coloration, features important in reproductive isolation and speciation, can be quantitatively analyzed across geography. Their degree of change can easily be compared with those for morphology and structural allelic frequencies (but see Lewontin 1984).

The usual fashion, however, in which specimens are gathered and prepared results in poor material for mosaic evolutionary studies. Typically, a researcher interested in comparing geographic variation in morphology with that in song for a given species uses available museum specimens

and/or collects additional new skins from a series of populations for the morphologic analysis and records vocalizations from different individuals of those same populations. Practical considerations usually prevent gathering both morphologic and vocal data from the same birds. Nonetheless, the best data relevant to mosaic evolution will be those on character correlations within individuals, not populations. Ideally, the systematist requires thorough information on vocal behavior, morphology, coloration, and genetic variation, among other parameters. But such comprehensive data are not easily obtained, using traditional methods, for individuals. Even for morphologic characters, workers routinely gather "skin data" and "skeletal data" from separate series of specimens because during skeleton preparation the skin characters for those individuals are lost. Clearly, researchers should attempt to devise procedures that allow retrieval of maximal data for each individual sacrificed. Such a goal is also compatible with wise conservation practice. To this end, we recommend the use of unusual kinds of preparations termed "skin-skeleton" specimens, described below.

For several years we have been applying a battery of research procedures to large samples of specimens of a number of avian taxa. This experience prompts us to describe field and laboratory techniques we have derived and found useful, methods that supplement procedures already published and widely known. We recognize that other workers may already be using more effective or efficient procedures than those we describe. We encourage them to inform colleagues (including us) of any such techniques in order to facilitate the proper growth of this research arena. Finally, we call attention to areas of procedure that continue to present difficulty.

PRESERVATION IN THE FIELD OF TISSUE SAMPLES FOR ELECTROPHORETIC ANALYSIS

Interval between death of bird and tissue preservation.—To prevent protein denaturation, tissue samples should be preserved by low temperature freezing as soon as possible after death, preferably within a few hours. More rapid freezing is required if ambient temperatures are over approximately 80°F (26°C). Specimens should be kept shaded and in well-ventilated containers before processing. It is better to keep whole specimens intact than to take tissues and not to freeze them immediately. This applies to specimens stored in a normal freezer; it is preferable that such specimens not be dissected until the tissues can be transferred, either to an Ultra-cold freezer or to a liquid nitrogen refrigerator for more permanent storage. Therefore, tissue samples should not be stored in a normal freezer. Responses of tissues to freezing are discussed by Mazur (1970).

Liver and pancreas contain enzymes (proteases) that digest other proteins. If these tissues are disturbed, these proteases may be dispersed and result in rapid destruction of the enzymes, in the liver and elsewhere, of interest to the researcher. Consequently, if a bird is shot in the abdominal (liver) area, it is especially important to process the specimen and to preserve the tissues in liquid nitrogen as soon as possible.

It is not known precisely what the maximum survival interval is for any enzyme under typical field conditions. It is established, however, that proteins vary greatly in their denaturation times at a given temperature. We have seen good activity in the laboratory from tissue held at room temperature or above for up to 8 h after death. Even longer periods of retained activity are likely for certain protein systems. Thus, even road-killed specimens may harbor at least some active proteins. There is need for much experimentation and sharing of findings in this area.

Type and quantity of tissue to preserve.—We routinely analyze heart, liver, kidney, breast muscle, and blood. These tissues allow us to score consistently 40± loci per species. Other workers have examined brain, testis, eye lens, and, most recently, actively proliferating feather pulp (Marsden and May 1984). Different tissue types contain different proteins (Harris and Hopkinson 1976). Again, laboratory experimentation is necessary to determine which tissues provide scorable bands for the particular taxon being investigated. For a bird the size of a sparrow, the entire heart, liver, kidney, and approximately 1 cc of breast muscle are sufficient for a plethora of gels. For larger species, especially those that are rare or difficult to obtain, as much tissue should be saved as storage space allows.

Tubes for tissue storage.—All the necessary tissues from a small (15 g) bird will fit easily into a single nunc tube (manufacturer's specifications and address of supplier: A/S Nunc biological test tubes, screw cap, silicone washer, size 2 cc, 38 × 12.5 mm, catalogue no. UCC-76; available from Almac Cryogenics, 1108 26th St., Oakland, California 94607 and from Thomas Scientific).

If liver and muscle are saved, it may not be necessary also to save blood. The additional proteins that can be obtained from blood, two hemoglobins and several general proteins from the plasma, may not be worth the additional effort. Nevertheless, if the loci are needed, the following procedure has worked under field conditions for one of us (GFB). A small centrifuge operated off a car battery (via an AC-DC inverter) or a hand-centrifuge (e.g., Thomas Scientific No. 2506-E05) can be used to separate red cells from plasma after blood is drawn with a heparinized syringe by cardiac puncture. For most birds, small amounts of blood (less than 1 cc) are obtained from shot specimens. Consequently, small vials are necessary

for storing the separated material drawn off from the centrifuge tube using a Pasteur pipette. Snap-top, polypropylene micro-centrifuge tubes of approximately 0.25–0.5 cc capacity can be used for this purpose.

Labeling and storage of nunc tubes.—Because the writing on frosty tubes can be extremely difficult to decipher, proper labeling of specimen tubes is of extreme importance. At the very least, label the tube with the initials and field number of the collector and either the common or scientific name of the bird (if known with certainty). Because of unfortunate experiences, one of us (NKJ) prefers to duplicate the field number in large numbers in the remaining space on the tube. We often use indelible marking ("Sharpie") pens; many other suitable pens are available commercially. The practice of scratching the information on the vial with a needle or other pointed instrument should be avoided. Such etchings are easily worn away and can become extremely difficult to read.

THE TEMPORARY STORAGE OF TISSUES IN THE FIELD

Dry ice.—When field time for specimen processing is limited, dry ice (−76°C) offers the convenience of temporary preservation of whole animals. For this purpose, a thick-walled, commercially available dry ice chest is preferred over a styrofoam cooler. One hundred lb (ca. 45.4 kg) of dry ice in such a chest will be sufficient for 1 week in the field under normal conditions (R. D. Sage, pers. comm.).

Liquid nitrogen.—During extended field work, storage in liquid nitrogen is the method of choice. At least 20 models of liquid nitrogen refrigerator tanks or dewars are available that are suitable for field storage and transport of tissue. These tanks can be obtained commercially from the Cryogenic Equipment Department of Union Carbide Corporation. Technical aspects of biological storage vessels using liquid nitrogen are discussed by Gareis et al. (1969) and in the Cryogenic Equipment catalogue and other brochures distributed by Union Carbide Corporation.

Models commonly in present use vary from those with a large storage capacity (LR-50, 130 lb when full, holds 50 l) and substantial static holding time (100 days) to tanks with medium storage capacity (XR-24, 81 lb when full, holds 29 l) and long static holding time (240 days). At the Museum of Vertebrate Zoology, University of California, Berkeley, two models are especially popular. The LR-17 weighs 50 lb (22.6 kg) when full (17.4 l) and has a static holding time of 48 days. The LR-10C is smaller (33 lb or 15 kg when full) and thus holds less liquid nitrogen (10.4 l) and less storage space, but has a longer static holding time (60 days) than the LR-17.

During 1983, Union Carbide Corporation introduced several new lines of liquid nitrogen refrigerators and dewars that offer improvements in cap

and necktube design and insulation. These tanks provide longer static holding times for a given volume of nitrogen than earlier models. The HCL series of refrigerators has large storage capacities (up to 34 l) and substantial static holding times (50–200 days). The XCL series offers tanks with capacities of 3–34 l and static holding times, varying with tank size, of 27–340 days. In addition, for the shipment of small quantities of biological specimens, the "3DS Dry Shipper" is available. It offers the convenience of relatively small size (holds 3 l, 15 lb [6.8 kg] when full, 15 in [38.1 cm] high, 7.6 in [19.3 cm] in diameter) with a respectable static holding time (20 days), and a positive-closure cap. Because it contains an adsorbent, samples are kept cold and dry at cryogenic temperatures and no liquid nitrogen is available to spill or leak. In addition to the "Dry Shipper," two models from the new series of tanks are especially suitable for avian systematic work, the 18-XT (comparable to Model LR-17 mentioned above), weighing 26.8 kg when full, 18 l capacity, and with a static holding time of 200 days; and 10-XT (comparable to LR-10C), weighing 15.4 kg when full, 10 l capacity, and with a static holding time of 111 days.

The LR-10C or 10-XT models are small enough to be transported in back packs or in pack saddles for mules. During such transport, however, it is important to maintain the tank vertically, for spillage occurs easily if the tank falls on its side. On long field trips in warm climates we have found it useful to start with two filled tanks (LR-10C). One tank is used for tissue storage; the other holds a reserve supply of liquid nitrogen. Because the first tank is opened frequently when tubes are added and frozen, the nitrogen level drops relatively quickly. Because the second tank is seldom opened, nitrogen evaporation from it is greatly reduced. When necessary, the second tank can be used to refill the first tank.

At a temperature of −320°F (−196°C), liquid nitrogen can be a dangerous substance, causing severe frostbite if it comes in contact with human skin. Instructions for its use (Form 9888-Q, Precautions and Safe Practices, Liquified Atmospheric Gases, December 1979, Linde Division, Union Carbide; see also Linde Publication F-9914), provided with the refrigerators, should be followed very carefully. For example, in the field it is important to be certain that the fluted necktube plug on the tank cap is adequately vented and free from obstructions such as frost or ice. Without proper venting, which allows the liquid to gasify directly into the atmosphere, pressure builds within the tank which then becomes, in effect, a bomb. Excessive bouncing of the tank or very humid conditions can also cause pressure increases.

Sources of liquid nitrogen.—Liquid nitrogen is available commercially in cities and, occasionally, can even be found in very remote towns. It is

a by-product of liquid oxygen production and thus is often sold by companies that supply the latter substance to welders and hospitals. In regions with active cattle and poultry industries, liquid nitrogen is used for the storage and transport of livestock semen and vaccines. College and university physics, chemistry, and agriculture departments often have supplies on hand for teaching and research purposes and will usually part with some in an emergency. The cryogenic industry, locally active in some regions, can also be a source. The Union Carbide Corporation produces a list of suppliers of liquid nitrogen in the United States.

Transport of liquid nitrogen on commercial aircraft.—Because it is a corrosive substance if it spills, liquid nitrogen is treated as a "restricted article" by airline companies. Thus, this preservative is troublesome baggage for researchers who travel by air to and from field sites, especially in foreign countries. Requirements of the United States Department of Transportation and IATA-ICAO (International Air Traffic Association-International Civil Aeronautics Organization) Dangerous Goods Regulations (24th ed.), in effect as of December 1983, are as follows:

To transport liquid nitrogen by aircraft, a form, the "Shipper's Declaration for Dangerous Goods," must be filled out in triplicate. Such forms can be obtained from airline cargo departments or from freight forwarding companies. One copy of the form must be attached to the liquid nitrogen container package and the other two copies are to be presented to the clerk of the carrier airline during check-in. The form must list the information required by the Department of Transportation Domestic Regulations (in 49-Code of Federal Regulations, Civil Aeronautics Board 82) or the International Air Traffic Association (IATA-ICAO) Restricted Articles Regulations, as shown below:

Heading on Form

"*Proper Shipping Name.*" Write "Nitrogen refrigerated liquid."

"*Class.*" Write "2 (non-flammable) UN 1977."

"*Subsidiary Risk.*" Write "NA."

"*Quantity.*" Here write the amount you ship, in liters. (Passenger planes allow up to 50 kg per package; cargo planes allow up to 500 kg per package.) Also, one must state, "Packed in cryogenic container with pressure release (vented) valve." In the appropriate place on the form, be sure to cross out the type of plane (passenger vs cargo) you are not using.

"*Additional Handling.*" Write "transitional."

"*Packing Instructions.*" Write "210." This is the section number in the IATA-ICAO 24th ed. for non-pressurized items.

In addition, the package should be labeled, (a) "This End Up," with

an appropriate arrow drawn in; (b) "Keep Upright"; (c) "Do Not Drop"; and (d) "Handle With Care." It is advisable to contact the carrier airline before arriving at the airport to inform them of your intention to ship "dangerous goods," to tell them that you are aware of the regulations governing such matters, and to stress that the liquid nitrogen is in a non-pressurized, cryogenic container. It is important to realize that the pilot has final say on what will be included as baggage or cargo on the aircraft he or she commands. We have found that the Restricted Article Department of Federal Express will often help in filling out the forms for shipments within the United States. Non-compliance with regulations governing the shipping of restricted articles can result in severe fines or imprisonment.

For international travel, if one knows of a dependable source of liquid nitrogen in the country being visited, it is a simple matter to take the empty tank as baggage, in which case no declarations need to be made. Upon returning to the United States, we have found it propitious to pour out all but a quantity of nitrogen sufficient to cover the filled nunc tubes in the bottom of the tank. This procedure significantly reduces baggage weight and the smaller quantity of nitrogen remaining (which still must be declared) usually seems less threatening to the airline desk clerk. Although tissue-filled tubes reportedly will stay frozen in the tank for up to 24 h, even after all of the nitrogen has been poured off, the real threat of mis-routed or otherwise delayed baggage dictates that at least a few liters should always be retained.

NOTES ON ELECTROPHORETIC METHODS

The notes to follow assume that the researcher has at least a beginner's familiarity with standard electrophoretic methods, such as those outlined by Yang (1971) and Harris and Hopkinson (1976). Many of the following procedures, however, are either not explicitly described in the literature or are in very scattered publications not usually read by avian systematists. Moreover, because each laboratory evolves certain local techniques appropriate to its particular needs, the source of a given protocol is sometimes unclear. Therefore, we acknowledge that some of the methods we describe were devised by others, especially Suh Y. Yang, Monica M. Frelow, and Richard D. Sage, at the Laboratory of Evolutionary Genetics, Museum of Vertebrate Zoology.

Preparation of whole-tissue extracts.—Thaw tissue samples and keep on ice (4°C). Always preserve some unground tissue and return it to the Ultra-cold freezer for storage. Once tissue is ground, its survival time is significantly lessened. Furthermore, repeated thawing and refreezing of tissue extracts is the primary cause of inactivity in enzymes. Mince ap-

TABLE 1
ELECTROPHORETIC CONDITIONS USED AT THE MUSEUM OF VERTEBRATE ZOOLOGY

Gel type[a]	Electrode buffer[a]	Volts	h	Tissue	Loci[a,b,c]
LiOH, pH 8.2	LiOH, pH 8.1	300	3	liver[d]	LGG; LA-1, 2; GDA; LAP; EST-1, 4; AB-1, 2, 3, 4
Tris Maleic, pH 7.4	Tris Maleic, pH 7.4	100	4	liver[d]	6-PGD, SOD-1, 2; G-6-PDH
Poulik, pH 8.7	Borate, pH 8.2	250	3	muscle	GPI; CK-1, 2; LDH-1, 2
Tris Citrate II, pH 8.0	Tris Citrate II, pH 8.0	130	4	muscle	ADA; MPI; GPD
				liver[d]	ICD-1, 2; PGM; GLUD; GR; GPT; ADH; SDH; ACON-1, 2; EAP; GOT-1, 2; NP; ME; MDH-1, 2

[a] Gel type, electrode buffer, and recipes for specific protein assays are described by Selander et al. (1971) and Harris and Hopkinson (1976).
[b] Abbreviations for loci follow Harris and Hopkinson (1976).
[c] Many loci are scorable on several gel/buffer types and with several tissues.
[d] All loci scorable with liver tissue are also scorable in kidney tissue. Occasionally, loci that yield indistinct bands in liver can be scored more clearly with kidney; thus, the reason for saving both kinds of tissue.

proximately 0.5 cm × 0.5 cm tissue with a razor blade on a glass plate, combine it with an equal volume of de-ionized water, and put the mixture into a labeled centrifuge tube. Some workers (e.g., Nakanishi et al. 1969) use a buffer solution in this process. This amount of tissue extract, once centrifuged (at 18,000 RPM for 20 min), will be sufficient for running at least 15–20 gels per individual. For some very concentrated enzymes, the extract can be diluted. Initially, prepare extracts of each tissue type separately for a few individuals and determine tissue and gel/buffer specificity of each protein to be assayed. Once optimal tissue/gel specificity is determined it will be possible to mince tissue types together to prepare the tissue extracts, thereby reducing the time and effort involved in preparing extracts.

Gel/buffer combinations and staining.—Experimentation reveals which loci are best scored on which gel/buffer combinations. See Barrowclough and Corbin (1978), Yang and Patton (1981), and Harris and Hopkinson (1976) for some starting points. In Table 1, we list the electrophoretic conditions in common use at the Museum of Vertebrate Zoology, University of California, Berkeley. These conditions have proved to be suitable for the analysis of over 2800 birds of 40 genera and 10 families. It is desirable to examine a locus on several gel types (e.g., Coyne et al. 1979, Aquadro and Avise 1982). However, we attempt to minimize the number of gel types needed to complete a survey. Our standard protocol for birds is eight gels for 40± loci.

Often a given slice of a gel can be stained for several enzymes. For example, we use a number of ultraviolet protein assays (e.g., EAP, EST-D, GSR). These gel slices can be rinsed with de-ionized water and treated with a visual stain for another protein. Several peptidases are routinely surveyed in birds and other vertebrates. The recipes for these assays differ only in the substrates used (e.g., leucylalanine, leucylglycyl-glycine). First, determine if the protein products of these peptidases have different mobilities on the gel. If so, then two substrates can be used at once in the same assay, resulting in multiple peptidases being scored on the same slice.

Always strictly follow the safety precautions given by the manufacturers of chemicals, such as those on the use of gloves and masks. It is important to note that some routinely used reagents are known or suspected carcinogens (e.g., L-LEUCYL-β-NAPHTHYL-AMIDE HCl, used in the stain for the LAP locus; o-DIANISIDINE, used in the stains for all peptidases; and α-NAPHTHYL ACID PHOSPHATE, used in the stain for acid phosphatase [AcPH]; M. M. Frelow, pers. comm.).

Our protein assays, like those of other workers, consist of several types: ultraviolet, "aqueous," and agar-overlay. In most instances we photograph stained gels of the latter two types, unless all of the individuals on a gel are monomorphic. Gels stained in a non-agar medium, except for UV assays, are dried with a paper towel, wrapped in plastic, and stored in a cold room for future reference. For agar-overlays, we make a filter paper "print." Within a few days after stopping the reaction with acetic acid, we drain off the remaining acetic acid, lay a piece of filter paper over the gel, and invert the box. This causes the gel, agar, and filter paper to drop out onto a paper towel, with the gel on top and the filter paper on the bottom. Because the bands are in the agar, the gel can be removed and discarded. Within 1 or 2 days, the bands will transfer to the filter paper as the agar evaporates and dries. The filter paper is then taped to a large index card, labeled, and saved for future reference (see Fig. 1).

Design of electrophoretic experiments and studies.—Electrophoretic experiments should be designed for maximal efficiency and economy. In our laboratory we put 18–20 individuals (a set) on a single gel. Rather than do 20 individuals for all loci (40 $\pm$ 5), it is much easier to run at one time multiple sets of individuals for a lesser number of loci. For example, we often run three sets of individuals on two gel types (i.e., six gels at a time). This procedure greatly reduces the number of protein assays to be prepared per experiment. The protein assay recipes then should be tripled and can each be prepared in a single flask. From each individual vial we dip two wicks, one for placement into each of the two gel types. The individuals must be ordered identically on the protocols (list of spec-

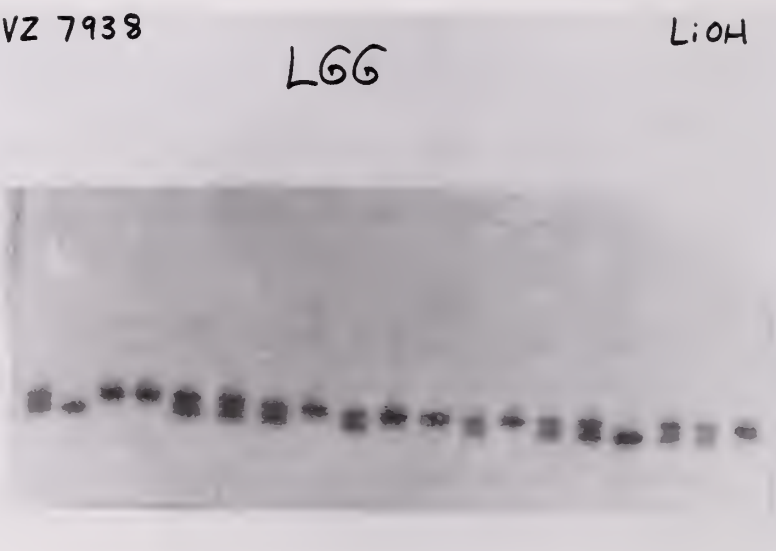

FIG. 1. Photograph of an agar-overlay preparation for LGG. Genotypes of 19 individuals of the Solitary Vireo (*Vireo solitarius*) are shown. From left to right the genotypes of the first four individuals are as follows: MS heterozygote, S homozygote, M homozygote, M homozygote, etc.

imens being run) for each gel type. That is, if we examine sets "a"–"c," using LiOH and TC 8 gels (three gels of each type), we load set "a," on LiOH and TC 8 gels at the same time.

In a large geographic survey, we often first examine a few birds from each population for a total of at least 45 loci. Loci showing sufficient variability either within or among samples are surveyed for all remaining individuals. However, for questions such as paternity analysis or selective neutrality of allozymes (e.g., Zink and Winkler 1983, Barrowclough et al. 1984), every individual must be scored for every locus. Sarich (1977), Nei (1978), and Gorman and Renzi (1979) discuss the number of individuals and loci needed for electrophoretic studies. In general, it is preferable to examine as many loci as possible, rather than as many individuals as possible. Different questions require, however, different sampling methods.

Computer routines for electrophoretic data analysis.—The proper analysis of electrophoretic data involves the equations of population genetics (e.g., Crow and Kimura 1970, Hartl 1981). A program package, BIOSYS (Swofford and Selander 1981), performs most calculations routinely used in electrophoretic studies. Other types of calculations can be found in

numerous papers in the literature (see summaries in Powell 1975, Nevo 1978, and the extensive bibliography in Smith et al. 1982).

"SKIN-SKELETON" PREPARATIONS

The importance of skin-skeleton preparations for phenetic studies was first recognized in the late 1960s and early 1970s by D. M. Power and R. F. Johnston at the University of Kansas and then generally implemented by J. C. Barlow and J. D. Rising at the Royal Ontario Museum in Toronto. With the development of biochemical methods for the study of geographic variation, it has now become of interest to compare patterns of variation of different sets of characters from the same individual specimens, to see if there is geographic concordance of varying attributes of a bird's phenotype and genotype. Thus, many avian systematists now require plumage, skeletal, and tissue data from each specimen. This need has led to the further development of non-traditional methods of preparing specimens in the field.

The following three descriptions of specimen preparation techniques permit one to take a complete range of both skin and skeletal measurements and tissue from the same individual. Each method has its advantages and disadvantages and we do not necessarily recommend one over the others. One of us (NKJ) prefers method 1; another (RMZ), method 2. Method 3 has been in use for many years by J. C. Barlow and J. D. Rising and their colleagues at the Royal Ontario Museum and University of Toronto. We emphasize that these detailed descriptions are of methods the authors have found to be suitable and efficient; other workers may develop variant procedures that are equally effective, or better, for their purposes.

Method 1.—In this procedure, the resulting specimen is a roughed out skeleton that retains its rectrices, primaries and secondaries, and their coverts, and the ramphotheca of the bill. The specimens are dried in the typical study skin posture (Fig. 2). All routine measurements (bill length, wing length, tarsus length, etc.) are taken from the specimen before it is prepared as a complete skeleton.

One distinct advantage of this preparation over the standard study skin is that the mandibles remain in perfect alignment. Such is rarely the case for study skins which have the mandibles tied by thread. A high proportion of museum specimens of many small birds have their lower mandibles improperly seated in the upper mandibles; thus, bill depth measurements are invalid. And, flat-billed small birds (e.g., many Tyrannidae) frequently have their relatively soft bills crushed by over-zealous preparators during the thread-tying procedure.

The steps for the preparation of specimens according to method 1 are

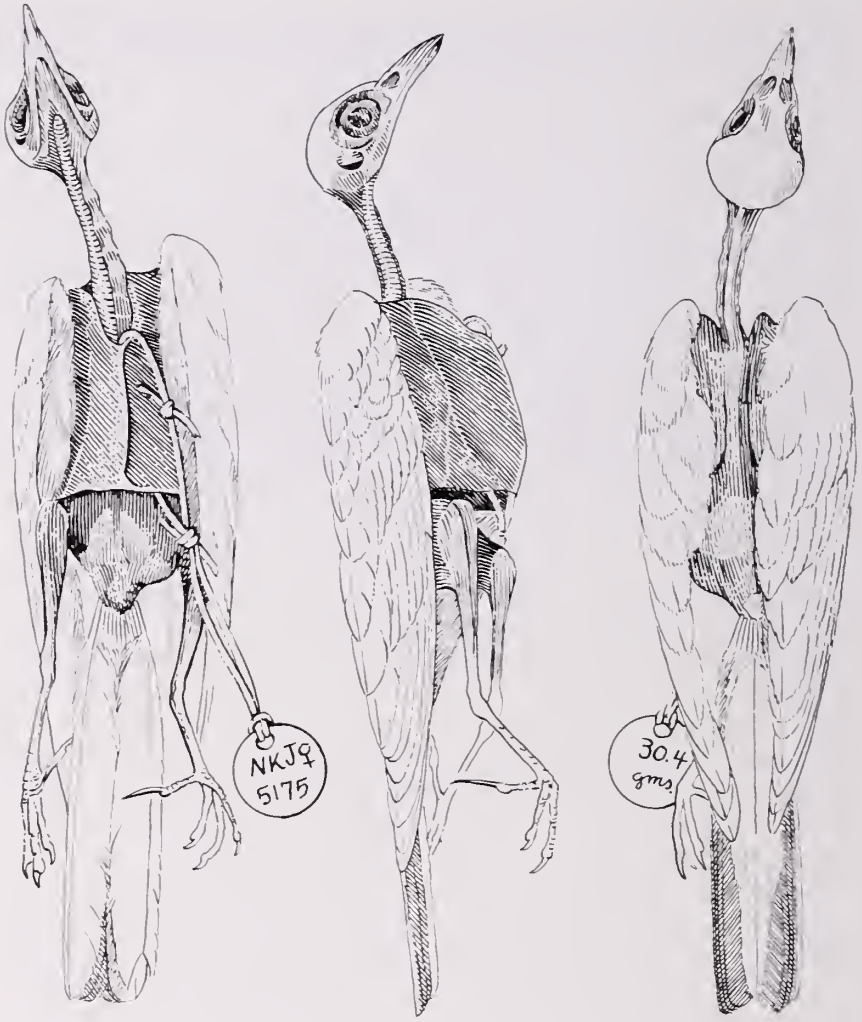

FIG. 2. Ventral, lateral, and dorsal views of a skin-skeleton preparation of a Horned Lark (*Eremophila alpestris*), specimen NKJ 5175, resulting from method 1. Sketch made directly from a dried specimen ready for measurement of skin features prior to being cleaned as a complete skeleton. A completed specimen tag (not shown) should be attached to the tibiotarsus. Note the position of attachment of the "skull tag."

as follows: make catalogue entry, label nunc tube, weigh specimen, and examine it for evidence of molt, ectoparasites, and external signs of breeding (incubation patch, cloacal protuberance). Fill out a stringed tag with collector's initials, field number, and sex symbol on one side, body weight

on the other and record data in field catalogue. "Skull tags," of high rag-content paper which is resistant to damage by immersion or dermestid beetles, the tags commonly used by mammalogists are suitable for this purpose. Limber specimen, first by rotating the head around the long axis of the body and then by gently extending each wing forward and then perpendicularly to body. Strip the skin from the head, starting from the ventral base of the neck, and pull skin toward the bill in successive strips. Note and record in catalogue the condition of the cranium with regard to relative pneumatization. Strip skin from the body: (a) pinch the patagium and pull skin off toward the body; (b) strip skin from humerus so as to leave this bone bare of feathers but retain all secondaries and their coverts and all primaries and their coverts intact on the wing in their natural positions; and (c) strip skin from body and from legs, proceeding caudally. If legs are broken take special precaution not to tear away the legs with the strips of skin and feathers.

With the tips of skinning scissors, cut through the body wall just posterior to the last rib and posterior to the caudal rim of the sternum. With the belly up, arch specimen in the hand to expose the internal organs. With curved forceps, pinch the heart away from its major blood vessels and place it near the labeled nunc tube. Sever the esophagus a few millimeters above its attachment to the stomach and place of attachment of the liver. Seize the posterior stub of the esophagus with forceps and gently pull the viscera out of the body cavity in one mass (while looking for the gonads from the left side) and sever the large intestine near the cloaca. This operation must be done with care so as not to disturb the placement of the gonads. Determine the sex of the specimen, measure the gonads, and record these data in field catalogue. Remove the lobes of liver from the visceral mass and place the liver next to the heart. Examine and record contents of stomach. Remove lungs from body cavity.

With tips of forceps, break through membrane lying between the arms of the furcula. This procedure leaves a hole, between the furcula and the neck, through which the string of the skull tag eventually passes. With curved forceps, lift entire kidney out of the body cavity and place it next to heart and liver. Cut away the breast muscle mass on both sides by incisions first running anteriorly along the keel of the sternum and sides of the furcula and then along the rib cage from the base of the keel to the humerus, where it meets the other incision. Great care must be taken not to cut through either the keel of the sternum or the arms of the furcula. Save as much undamaged breast muscle as desired; a piece 12 mm × 12 mm × 6 mm is suitable for a small nunc tube. Place the piece of breast muscle near the other three tissues from the same specimen.

Place the four types of tissue into the labeled nunc tube in the following

order: (a) heart, which fits well into the rounded bottom of the tube; (b) liver; (c) breast muscle; and (d) kidney. The exact sequence of storage is not crucial, but it is helpful if the sequence of each preparator is known to the laboratory worker who will analyze the tissue. Liver and kidney tissue can be difficult to distinguish when frozen and, thus, should be kept separate in the tube. Some workers prefer to store each tissue type in a separate tube; in general we have not found this procedure to be useful. Avoid packing tissue tightly into the nunc tube because overly-crowded tubes easily shatter when placed in liquid nitrogen.

Enter sex symbol on skull tag and complete catalogue entry. Insert one string of the skull tag into the body cavity and out through the opening between the furcula and the neck. Tie the skull tag with two overlapping square knots. Do not tie the tag tightly around the sternum and furcula because the soft and flexible keel of the sternum and arms of the furcula may be crushed and/or distorted and may dry in unnatural positions. Firmly attach completed specimen tag to the tibiotarsus using two overlapping square knots. Arrange specimen for drying by folding wings along sides of body as in an ordinary study skin. Place specimen in a well-ventilated but insect-proof container. Clean instruments before next specimen is started to avoid mixing fragments of tissue and blood from different individual birds.

Method 2.—This method describes the preparation of a complete study skin and partial skeleton from the same individual. Many details overlap with method 1. One important difference is that in this procedure the tissue samples are removed before the specimen is prepared. First, weigh specimens, label them plus nunc tubes, and record data in field catalogue. Slit the ventral skin covering the abdomen and separate the skin from the body, as in the preparation of a typical study specimen (see Hall 1962: 26–35). Make another ventral slit into the body cavity, thereby exposing the internal organs. Remove liver and heart samples through this slit. Remove gizzard and intestines. Avoid damaging gonads, which can be difficult to find on non-reproductive individuals, and avoid soiling the feathers surrounding the ventral opening. Stomach contents can be preserved at this time. Remove kidney sample and then push skin up slightly on body, exposing enough pectoral muscle for a sample. Place tissue samples in labeled nunc tube as soon as they are taken from the body. Determine sex and record condition of the gonads. Put sawdust or cornmeal in and around opening to prevent soiling of feathers (for skin preparations only). Secure label to specimen and set it aside. Once eviscerated, specimens can be prepared as skins or skeletons, either immediately or up to several days after removal of tissues, especially if the birds are kept cool. This procedure allows tissue samples to be taken from up to a dozen individuals in a relatively short time. On short autumn or winter days,

extraction of tissue from all specimens as described permits one to spend as much time as possible afield during daylight hours; specimen preparation can be completed after dark.

Standard methods (Hall 1962) of study skin preparation are then followed, except: (1) dissect out and set aside one tibiotarsus. This requires everting the skin over the juncture of the tibiotarsus and tarsometatarsus, whereas normally one stops before this point. Replace the tibiotarsus with a wooden stick of equivalent length, and wind an appropriate amount of cotton on it to simulate the normal leg; (2) when the wings are reached in the skinning process, use a scalpel to dissect out an ulna from one wing and a radius from the other wing; set these bones aside with the tibiotarsus if they become detached from their connections to the humerus. This procedure necessitates "stripping" the secondaries from the ulna, a practice which otherwise should be avoided because it distorts the natural alignment of the secondaries on the finished skin. At this point, one usually ties together the distal ends of the ulnae or the humeri, so that the wings are more firmly attached to the rest of the skin. However, in this procedure, place a thread with a slip knot at one end around the distal end of the ulna and tie it to the opposing distal end of the radius, on the other side of the body, at a distance about equal to the distance between the heads of the humeri in the intact body. In the event that the ulna and radius must be taken from the same side, the wings can be tied together by running a threaded needle through the skin of the inverted wing near the distal end of the ulna, i.e., near the junction of the ulna/radius and carpometacarpus. (3) Continue with standard procedures by working the skin over the head, but remove the eyes and set them aside with the excised tibiotarsus. With a knife, sever the skull (in cross section) near the anterior part of the orbits; however, do not cut the tongue and hyoid apparatus; the latter elements are left with the trunk skeleton. This allows the distal one-half of the skull to be preserved. The sharpened end of a stick, with an amount of cotton that approximates the size and shape of the body, is then seated firmly into the base of the upper mandible. Complete preparation of the study skin. Although much of the skull has been removed, the skin shows no apparent ill effects. The cotton eyes can be made somewhat larger than usual to support the skin in the absence of the cranium. Using fine thread, loosely wrap the trunk skeleton and the leg bones, after placing the eyes (and wing bones if detached) inside the body cavity. Attach a label bearing the same field number as that on the nunc tube and skin. Allow skeleton to dry out of sunlight.

Method 3.—As a further variant, it is possible to preserve a study skin with a partial skeleton, in which complete leg and wing skeletal elements are left in the skin on only one side (Barlow and Flood 1983). J. D. Rising (in litt., 17 May 1984) has kindly supplied the following information on

this method: as in other methods, the specimen is weighed, selected measurements are taken, etc. Then, the bird is skinned out over one side. Distal-most bone elements are left in the appendages on one side (viz. carpometacarpus; foot and tarsometatarsus, and perhaps one-half of the tibiotarsus). If the bird has been shot, the preparer may elect to leave "broken" elements on the skin-side of the specimen; it is even possible to leave the wing from one side with the skin and the leg from the other.

As soon as the skin is removed from the carcass, tissue samples can be removed and frozen. The skin can then be prepared as a conventional study skin, minus one leg and one wing, and the bill, or prepared as a flat skin. In the field, generally, the skin is salted later to be washed and cleaned in an organic solvent in the lab. The bill is with the skeletal part of the specimen. The mandibles will remain in perfect alignment and can be measured at any time prior to sending the skeleton to be cleaned. This method gives a study skin, nearly complete skeleton, and opportunity to easily remove tissues, assess gonads and stomach contents, and is fast. An average skinner can do five to eight birds an hour.

With experience, certain of these procedures can be combined or modified to suit the individual needs of the investigator. For example, tissues can be taken from all specimens prior to preparation regardless of the method used to prepare skins and skeleton. It might be desirable in some instances to measure the wing and tail in the field prior to preparations of specimens as complete skeletons. One of us (GFB) preserves a complete skeleton and a partial flat skin (minus wings) from each individual; the latter are used for studies of dorsal, flank, head, and throat coloration of juncos.

These techniques all share a common goal—to preserve as much material as possible from each specimen, given time constraints. Considering the prevalence of anti-collecting attitudes and widespread habitat destruction, it is difficult to justify the preservation of only study skins, as was historically prevalent. At the least, a "trunk" skeleton should be saved along with the standard study skin, whenever possible.

SUMMARY

We discuss several procedures suitable for the needs of modern systematic ornithology, with emphasis on electrophoresis and specimen preparation. Specifically, we describe: (a) methods for the sampling, preservation, and transport of tissue in liquid nitrogen; (b) available liquid nitrogen storage vessels; (c) regulations governing the transport of liquid nitrogen aboard commercial aircraft; (d) techniques useful in the preparation of whole-tissue extracts, gel/buffer combinations and stains, and the design of electrophoretic studies; and (e) methods for the preparation of "skin-skeletons," specimens that allow all routine skin and skeletal measurements and tissue to be taken from the same individual, thereby maximizing the informational content of every specimen.

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ADDENDUM

While the present paper was in press, the following articles appeared, each of which contains information relevant to one or more of the topics we discuss:

BUTH, D. G. 1984. The application of electrophoretic data in systematic studies. Ann. Rev. Ecol. Syst. 15:501–522.

DESSAUER, H. C. AND M. S. HAFNER (compilers and editors). 1984. Collections of frozen tissues: Value, management, field and laboratory procedures, and directory of existing collections. The Association of Systematics Collections, Univ. Kansas, Lawrence, Kansas.

MATSON, R. H. 1984. Applications of electrophoretic data in avian systematics. Auk 101: 717–729.

MOORE, D. W. AND T. L. YATES. 1983. Rate of protein inactivation in selected mammals following death. J. Wildl. Manage. 47:1166–1169.

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OBSERVER AND ANNUAL VARIATION IN WINTER BIRD POPULATION STUDIES

Paul G. R. Smith

There are many factors which influence the results of avian censuses and surveys and thus affect the comparability of results across plots (Weber and Theberge 1977, Shields 1979, Ralph and Scott 1981). For example, the time (Shields 1977), duration (Engstrom and James 1984), and date of survey (Järvinen et al. 1977), the experience (Faanes and Bystrak 1981) and hearing ability (Cyr 1981) of observers, weather conditions (Falk 1979), and plot size (Engstrom and James 1981) are all known to affect survey results. If valid inferences are to be made concerning avian populations and communities by censusing different plots, the variation due to these factors must be assumed to be much less than the between-plot variation. Such an assumption is often made for between-observer and between-year variation in census results. If in fact these assumptions are invalid, erroneous inferences may result.

Variation due to observer and year of survey in breeding season studies has been examined by several authors (Enemar et al. 1978, Rotenberry and Wiens 1980, Ralph and Scott 1981, Wiens 1981a). The effects of these sources of variation on survey results in non-breeding communities, using methods such as the Winter Bird Population Study (WBPS), have never been investigated.

The WBPS is a method of estimating bird species' abundances during winter on sample plots (Kolb 1965). Several surveys (generally 6–10) are made of a plot during which the identity and location of each bird encountered is noted on a map of the plot. Many of the plots surveyed using this method are published annually in American Birds. Detailed descriptions of the WBPS method are presented by Kolb (1965) and Robbins (1972).

Differences between observers in WBPSs may be smaller than in breeding season studies due to the decreased importance of aural detection cues, so critical in breeding season studies (Cyr 1981, Faanes and Bystrak 1981). Large between-year environmental variation is thought to result in increased variation in species' populations (Järvinen 1979). Thus, inter-year differences in winter bird assemblages could be much larger than in breeding communities due to the larger between-year environmental variation.

In the present paper I test the hypothesis that the variation between observers and years in WBPSs may in fact be large enough, relative to

between plot variation, to introduce considerable bias into comparisons between plots. The results of this test have implications for the use of the WBPS method in ecological surveys and environmental impact assessment.

METHODS

Study plots and field methods.—Seven plots were sampled for this study: Sherwood, Cedarvale, Bayview, Park Drive, Rosedale, Upper Gerrard, and Chatsworth. All plots are located in Toronto, York RM, Ontario. They are urban habitat islands occupying river valleys and contain varying proportions of wooded and open habitats. Full descriptions of the plots are given in Smith et al. (1982). Three of the study plots were sampled in 2 successive years: Sherwood, Cedarvale, and Bayview (Table 1). During the second year, three observers independently sampled the Sherwood plot (Table 1). The three observers differed considerably in their ornithological experience: observer GF had over 40 years bird-watching experience and had conducted many breeding bird censuses (BBCs) and breeding bird surveys; observer PS had about 10 years bird-watching experience and had conducted several BBCs and WBPSs; observer DK had about 2 years bird-watching experience and had conducted one WBPS. The years of coverage of each plot and the number and initials of observers who conducted the sampling are detailed in Table 1.

Bird surveys were conducted according to the WBPS method outlined by Kolb (1965) and Robbins (1972) with the modifications noted in Smith et al. (1981). Between 5 and 10 counts were conducted on each plot. Time and weather information was recorded and the identity, number, and location of all birds noted on base maps of each plot. Summaries of the results of the WBPSs are given in Smith et al. (1981, 1982).

During the survey of Sherwood by three different observers, special precautions were taken to avoid confusing observer differences with differences due to other factors. Survey route and time of day (morning 07:30–11:00) were standardized. Wind velocity (Beaufort scale), ambient temperature, and percent snow and cloud cover were measured as potential covariates. Maximum and minimum temperatures were obtained from a local weather station, also as potential covariates. A non-parametric multivariate rank test (Puri and Sen 1971: 187) for all the above variables revealed no significant differences in the conditions and timing of surveys by different observers. Any differences in WBPS results can thus be attributed to actual differences among observers. Differences in personal methodology were not minimized as this experiment was a test of how important these differences may be. Specific differences are mentioned below.

Sampling design and statistical methods.—The WBPSs conducted for this study are organized as three separate "experiments" or sample surveys. These sample surveys estimate variance due to plot, year, observer, and sampling error. The sampling of three plots by the same observers in two successive years conforms to a 3×2 completely randomized factorial design. Both among-plot and between-year variation are estimated in this sample survey. However, among-plot variance cannot be separated from among-observer variation. The sampling of four plots in 1 year by one observer conforms to a four treatment, single factor, completely randomized design (Steele and Torrie 1980:137). From this set of surveys among-plot variance was estimated. The one plot sampled in one year by three observers is equivalent to a three treatment, single factor, completely randomized design (Steele and Torrie 1980:137). Among-observer variance can be estimated using these results. All of these designs estimate sampling error.

The estimation of sampling error in bird surveys often involves replication in space or, as in this case, replication in time (Gates 1981). The problem with these types of replication

TABLE 1
A LIST OF STUDY PLOTS INDICATING THE OBSERVERS AND YEARS OF COVERAGE FOR EACH

Plot	1979–80	1980–81
Sherwood	1 (GF)[a,b]	3 (GF, DK, PS)[a,b]
Cedarvale	1 (DK)	1 (DK)
Bayview	1 (DB)	1 (DB)
Park Drive	1 (PS)	—
Rosedale	1 (PS)	—
Upper Gerrard	1 (PS)	—
Chatsworth	1 (PS)	—

[a] Number of observers in each year.
[b] Observers' initials in parentheses.

is that each sample is not independent of the others and hence, sampling error is underestimated (Gates 1981, Rice 1981). As a result, inferences made on the basis of such estimates of sampling error can be subject to Type I errors (i.e., the rejection of the null hypothesis when in fact it is true). Despite these problems, replication in time is one of the few means of estimating variance in bird surveys and is widely used (e.g., Enemar et al. 1978, Anderson et al. 1981, Robbins 1981, Skirvin 1981).

A number of statistical methods were used in the analysis of the bird survey data. The primary statistical tool employed was analysis of variance, both parametric (Steele and Torrie 1980) and non-parametric (Puri and Sen 1971). Parametric analysis of variance was used when its underlying assumptions were met. These assumptions are that the dependent variable is normally distributed and that its variance is homogeneous within the different cells of the design (Steele and Torrie 1980:167). When these assumptions were not met, non-parametric methods were used. The use of analysis of variance tests the importance of plot, observer, and annual variance relative to sampling error. To examine the importance of plot, observer, and annual variance with respect to each other I used the *F*-test for comparing the estimated variances from different "experiments" (Snedecor and Cochran 1980:252). An assumption of this test is that the sampling errors of the different "experiments" are equal. This assumption was tested using the same *F*-test. The power of all the statistical tests was limited by the small number of observers, plots, and years used.

Two other statistical techniques were applied to the data prior to analysis of variance. These techniques were "jackknifing" (Routledge 1980, Smith and van Belle 1984) and rarefaction (Simberloff 1978, Tipper 1979). These methods relate to the measurement of diversity and will be outlined below in that context.

Variables used.—To analyze the importance of observer and annual variation, a series of variables were selected. These variables are commonly used in the analysis of bird survey data. The analyses can conveniently be divided into analyses of avian community composition, community structure, and species population densities. Community composition is used here to refer purely to the identities of the species which compose the communities and the between-plot variation in the identity and abundance of these species. Conversely, community structure is defined here as those aspects of community organization which are unrelated to the species composition. Community structure parameters frequently used are: overall avian abundance or density, number of species, the frequency distribution of the species' relative densities, and associated measures of diversity and evenness.

Diversity is a concept which includes the two components, number of species or species

richness, and evenness, the degree to which each species is equally represented in the community. There is a large, often acrimonious, literature on the measurement of diversity (for example see Dennis et al. 1979). A great many indices have been used and their relative merits debated (Hill 1973, Pielou 1975, Simberloff 1978, Patil and Taillie 1979, Alatalo 1981, Siegel and German 1982). Many diversity indices combine richness and evenness into one index. Hill (1973) and Patil and Taillie (1979) have both shown that many of these diversity indices are related and vary primarily in the weight placed on rare species. These measures of diversity are dependent on sample size. This dependency has led to the use of rarefaction as an alternative to diversity indices (Simberloff 1978, James and Rathbun 1982). Rarefaction is a statistical means of estimating the number of species expected in a random sample of individuals from a collection (James and Rathbun 1982). The method allows the comparison of the species richness of collections or samples with varying numbers of individuals.

In light of the variety of means to measure community diversity, four widely used methods were employed here. The number of species per survey was used as a simple indicator of species richness. Two indices which incorporate evenness were used, H' ($-\Sigma\ p_i \ln p_i$) and N_2 ($1/\Sigma\ p_i^2$). These indices are both subject to bias when based on a small sample and may have a non-normal frequency distribution. The jackknife statistical procedure can be used to remove bias, stabilize the frequency distribution, and provide an estimate of the variance of H' and N_2. Simply put, the jackknife procedure involves deleting one replicate, pooling all other samples, and calculating the indices. Each sample is deleted in succession. The full details of jackknifing are given by Routledge (1980). Jackknifed estimators of H' and N_2 were calculated using a FORTRAN program written by the author. The fourth method used to measure diversity was rarefaction. The expected number of species [$E(S_n)$] in a random sample of n individuals drawn from N individuals (where $n < N$) was calculated for each survey. From the total number of birds on each survey (N) the number randomly selected (n) was varied from five by increments of five to the closest value to N. The calculations were performed using a FORTRAN program based on that in Simberloff (1978). The method of calculating $E(S_n)$ for each plot corresponds to the replication model outlined by Tipper (1979). Because the total number of birds, N, varies from survey to survey, $E(S_{15})$ was used for most statistical tests. Fifteen was the largest value of n for which $E(S_n)$ can be calculated for virtually all the surveys. A "knot-by-knot" comparison (sensu Tipper 1979) of the complete rarefaction curves of different observers and years was made using multivariate analysis of variance (MANOVA).

Two measures of evenness were applied to the data, $E_{2,1}$ [N_2/N_1] (Hill 1973) and $F_{2,1}$ [$(N_2 - 1)/(N_1 - 1)$] (Alatalo 1981). These variables were calculated from the jackknifed estimators of N_1 [$\exp(H')$] and N_2. Total number of birds detected per survey divided by the area of the plot was the measure of total avian abundance. This variable was log-transformed to meet the assumptions of analysis of variance.

The examination of differences between plots, years, and observers in the species composition of avian surveys is one of multivariate differences between "treatments." Hence, multivariate analysis of variance is the most appropriate method for statistical analysis (Stroup and Stubbendieck 1983). However, many species' abundances did not conform to the normal distribution, even after transformation. As a result, a non-parametric multivariate rank test (Puri and Sen 1971, Sarle 1983) was used to compare variance due to observers, years, and plots to sampling error. Observer, year, and plot differences could not be compared to each other with these data. To investigate such differences several observers must conduct WBPSs on several plots in several years.

To test the importance of observer and annual variance in estimating species' densities it was necessary to select species which were common during both years, on all plots, and

TABLE 2

COMPARISON OF OBSERVER, ANNUAL, PLOT, AND SAMPLING VARIANCE AS SOURCES OF ERROR IN ESTIMATING COMMUNITY STRUCTURE

Variable	Observer vs sampling variance (df = 2,20)	Annual vs sampling variance (df = 1,42)	Plot vs observer variance (df = 3,2)	Plot vs annual variance (df = 3,1)	Annual vs observer variance (df = 1,2)
Total density	0.39[a]	24.65[b]***	20.15*	0.90	51.34*
Diversity					
Number of species per survey	1.58	17.13***	2.42	0.07	10.38
H'	1.18	4.51[b]*	5.05	1.75	2.88
N_2	0.43	0.88	22.64*	47.31	3.24
$E(S_{15})$	0.08	0.45	20.45*	3.30	6.19
Evenness					
$F_{2,1}$	0.05	0.02	60.94*	317.53*	0.21
$E_{2,1}$	0.26	1.27	59.41*	32.62	1.87

[a] *F*-ratios of the variance due to the first factor to that due to the second.
[b] *** $P \leq 0.001$, * $P \leq 0.05$.

in surveys by all observers. This was needed to meet the assumptions of analysis of variance. On this basis six species were chosen: Downy Woodpecker, Blue Jay, Black-capped Chickadee, White-breasted Nuthatch, Northern Cardinal, and Dark-eyed Junco (see Appendix for scientific names). The species' densities were log-transformed to normalize their frequency distributions and stabilize their variances.

RESULTS

The results of comparing the variances attributable to different factors are presented in Tables 2 and 3. Values given in the tables are *F*-ratios or the ratios of the variances from two different sources. These values form the basis of the statistical tests and are an indication of the relative size of variances from the two sources.

Community structure—observer variance.—Observer variance was not significantly larger than sampling variance for any measure of community structure (Table 2, column 1). A comparison of rarefaction curves ($E[S_n]$ for $n = 5, 10, 15, 20, 25$) for the three observers using a multivariate analysis of variance also revealed no significant difference between observers ($F = 1.59$, $P = 0.17$). Between-plot variance was between 2 and 60 times greater than observer variance and significantly larger for total density, N_2, $E(S_{15})$, $E_{2,1}$, and $F_{2,1}$ (Table 2, column 3). The ratio of annual variance to observer variance was highly variable between measures (Table 2, column 5). Annual variance was significantly greater than observer variance for total density but not any other community structure variables.

TABLE 3

COMPARISON OF OBSERVER, ANNUAL, PLOT, AND SAMPLING VARIANCE AS SOURCES OF ERROR IN ESTIMATING SPECIES ABUNDANCES

Species	Observer vs sampling variance (df = 2,20)	Annual vs sampling variance (df = 1,42)	Plot vs observer variance (df = 3,2)	Plot vs annual variance (df = 3,1)	Annual vs observer variance (df = 1,2)
Downy Woodpecker	1.23[a]	0.01	1.60	231.00*	0.01
Blue Jay	0.17	0.00	31.62*	4535.33*	0.01
Black-capped Chickadee	4.68*	13.81***	5.44	1.50	3.63
White-breasted Nuthatch	1.54	7.57**	22.92*	1.05	26.02*
Northern Cardinal	1.84	12.51**	3.10	0.49	6.31
Dark-eyed Junco	0.21	6.85*	33.39*	0.75	44.48*

[a] *F*-ratios of the variance due to the first factor to that due to the second.
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.

Thus, confounding of annual and observer variation appears more serious than confounding observer and plot variation.

Community structure—annual variance.—Some measures of community structure showed a strong annual effect while others did not. Annual variance in total density, the number of species per survey, and H′ were significantly greater than sampling variance (Table 2, column 2). In addition, a comparison of the rarefaction curves ($E[S_n]$ for n = 5, 10, 15, 20, 25, 30, 35) for different years and plots combinations using MANOVA revealed a significant difference between years ($F = 2.56$, $P = 0.03$). However, between-year differences in N_2, $E(S_{15})$, $E_{2,1}$, and $F_{2,1}$ were not significantly greater than sampling error (Table 2, column 2). Between-plot variance in N_2, $E_{2,1}$, $F_{2,1}$, $E(S_{15})$, and H′ was greater than annual variance but significantly only for $F_{2,1}$ (Table 2, column 4). For total density and number of species per survey, between-plot variance was smaller than annual variance (Table 2, column 4). Summarizing, between-year variation is a substantial source of variation and thus comparisons between plots sampled in different years should be made cautiously.

Community composition.—Overall estimated community composition was not significantly different between observers (multivariate rank test, $\chi^2 = 40.0$, df = 41, $P = 0.51$). Four of the 24 species, however, showed significant univariate differences among observers. The four species were Mallard, Screech Owl, Black-capped Chickadee, and American Goldfinch. Differences in detecting Screech Owls were due to the use of a tape recording by observer GF. Differences in the numbers of goldfinches appear to be related to perceptual difficulties in estimating numbers of each species in mixed flocks of siskins and goldfinches (compare the results of the ob-

servers in the Appendix). Observer PS made special efforts not to double-count individual Black-capped Chickadees due to their tendency to follow the surveyor. This resulted in his substantially lower estimate of the abundance of this species (Table 3 and Appendix).

Overall community composition was not significantly different between years (multivariate rank test, $\chi^2 = 43.05$, df = 34, $P = 0.14$). However, 16 of the 34 species showed significant univariate differences between years.

The magnitude of observer, plot, and annual variance in estimating community composition cannot be compared here due to the limited nature of the experiment (see Methods). Although only small observer differences were observed here, caution is necessary in interpreting compositional differences, particularly if observer and plot variation cannot be separated. Compositional differences between years may be considerable and a larger sample of years could be used to examine this in more detail.

Species populations.—As might be expected, the effect of observer and annual differences was quite variable among species, as shown in Table 3. Differences between years tended to be substantially larger than between observers (Table 3, columns 1 and 2). Between-plot variation was significantly greater than that between observers for three of the six species examined (Table 3, column 3). The plot/annual and annual/observer variance ratios were highly variable among species (Table 3, columns 4 and 5).

Confounding observer variance with plot variance appears less serious than confounding observer and annual variance. But observer variance was up to 60% as large as plot variance. Thus, comparisons of the abundances of common species in WBPSs from different plots surveyed by different observers should be done with caution. A knowledge of between-observer and between-plot variance is necessary to rigorously interpret such comparisons.

DISCUSSION

In any ecological survey which uses data from different observers and years there are biases introduced which may obscure real ecological patterns. How important these and other sources of bias are is a function of the amount of variation between the samples or plots within the whole survey. As beta diversity and between-plot variation in community structure increases, the importance of other sources of error decreases. The analyses presented in this paper illustrate how the importance of such biases may be examined.

Other evaluations of the WBPS method have focused on its efficiency and sampling adequacy for estimating community structure and species'

abundances (Brewer 1972, 1978; Robbins 1972, 1981). Robbins (1972, 1981) has examined the question of what constitutes a sufficient number of replicates for the estimation of species abundances. Clearly, the validity of between-plot comparisons of species' abundances is dependent on factors such as: the abundance, frequency of occurrence, and other species' characteristics, the size of between-observer, between-plot and sampling variances, and the number of replicates in each WBPS. It is apparent from Robbins' (1981) work that the number of replicates needed to reasonably estimate species' abundances is larger than for estimating community structure. This may be particularly true if jackknifed estimators of community structure are used (also see Routledge 1980, Smith and van Belle 1984). Such estimators remove bias due to small sample size. The use of jackknifed estimators of species' abundances may also be a means of increasing the accuracy of estimating these quantities.

Observer variation.—A number of studies have found observer variation to be rather small in breeding season studies using the mapping method (Enemar 1962, Snow 1965, Hogstad 1967, Enemar et al. 1978). These studies have used only observers of considerable competence. Other authors have found substantial differences between observers with varied levels of experience (Faanes and Bystrak 1981, O'Connor 1981). None of these studies has considered the magnitude of observer variation relative to that source of variation which is of most importance to the particular study.

Studies of observer differences have for the most part focused on differences in estimating community structure or individual species populations. Faanes and Bystrak (1981), however, used a distance measure to examine overall observer differences in estimating composition. With the increasing use of multivariate statistical techniques to analyze avian community data it is important to investigate the effect of observer bias on such analyses. Hall and Okali (1978) examined the effect of observer bias on the extraction of compositional gradients in vegetation data using principal component analysis. They found that observer bias obscured several gradients actually present in the data. Results presented here indicated little difference in estimating community composition between the observers used. This may not always be the case and should be tested in each investigation.

Many of the sources of error identified in census work in breeding avian communities are equally important in surveying winter bird assemblages. Some of these sources of error, such as weather variables and time and duration of survey, can be controlled and/or statistically tested to detect differences between plots, as was demonstrated here. The estimation of observer variation requires field trials, but these are required if the WBPS is to be applied rigorously. In the present study, not all observers involved

in the larger study were tested but those representing the full range of experience were.

The results presented here suggest that observer variance in WBPSs may be less than in breeding season studies. This may be due to the reduced importance of aural cues—the use of which requires considerable expertise, lack of obstructing vegetation, and decreased species richness (alpha diversity). However, observer variation is primarily due to perceptual and methodological differences between people and thus will vary with the set of observers used.

Annual variation.—Annual variation in ecological communities and its effect on the testing of hypotheses have recently attracted considerable attention (Rotenberry and Wiens 1980; Anderson et al. 1981; Wiens 1981a, b; Rice et al. 1983; Rogers 1983). Many studies have noted substantial annual variance in avian community structure (Anderson et al. 1981, Wiens 1981a). Others, such as Järvinen and Väisanen (1976) assert that certain community structural features, e.g., diversity, vary little between years while features such as density vary considerably more. Furthermore, Anderson et al. (1981) have shown that the magnitude and direction of annual change in community structure can be different on different plots.

The importance of annual variation is obviously a function of the scale of the study as well as the quantity and heterogeneity of the data employed. The data presented here illustrate that, within the current study framework, annual variation is a substantial souce of variance. Its importance must be assessed within the context of each study.

Rotenberry and Wiens (1980) noted no significant differences in breeding bird community composition between years that differed considerably in environmental conditions. Data presented here indicate that substantial compositional change may occur in winter bird assemblages between years.

High annual variability in environmental conditions has been linked to high species turnover rates and greater variation in avian community structure (Järvinen 1979). Annual variation in the avian community in highly variable environments may be as important as spatial variation. Annual variation in community structure and composition may be due to any number of factors, e.g., local and/or large scale variation in individual species populations. Wiens (1981b) suggests that large annual variation may be due simply to a random redistribution of territories in unsaturated habitat. Whatever its source, such variation cannot be assumed to be small relative to between-plot variance.

Wiens (1981a) examined the effects of inter-year variation in census results on the testing of an hypothesis relating community structure to environmental variables. His treatment shows that such variation can

influence inferences which are made using plot data. Ignoring this variance could lead to results that are artifacts of the methodology.

In the years since its inception, many plots have been sampled using the WBPS method. Yet very little analysis and hypothesis testing have been done using these data. This contrasts markedly with the number of studies using data from breeding bird censuses. This is partially due to the relative scarcity of tests of the method's sensitivity to bias, compared to the exhaustive testing of methods used in breeding season studies. At the same time, WBPSs increasingly are being used in the environmental impact assessment process to document the effects of development or management policies on avian populations and communities. Ignoring the sources of bias in the WBPS method can only decrease the credibility of such assessments.

As the sources of bias in the WBPS are critically examined, the method can be refined to reduce the effect of such sources of error. Thus, users of the method may be able to apply it in a more rigorous manner.

SUMMARY

The assumption that observer and annual (between-year) variation in winter bird population studies (WBPS) results is small relative to between-plot variation was examined. The implications of the results for the use of the WBPS for hypothesis testing in ecological surveys and environmental impact assessments are discussed.

Data from a survey of winter avian assemblages in urban areas were used to test the hypothesis. Variables often used in avian community analysis were examined. Measures of community structure included several indices of diversity and evenness and overall abundance. Species composition was investigated using a multivariate rank test. Variation in estimating the abundance of six common species was also examined.

Observer variation in estimating community structure, community composition, and species' abundances was found to be small relative to both sampling and between-plot variance. Thus, in the context of the present study, observer bias did not appear important except in estimating number of species per count and H'. Annual variation in community structure, composition, and species' abundances was relatively large for many variables. Annual variance was seldom smaller than observer variance and only sometimes less than variance between plots. Thus, comparisons between plots surveyed in different years or between surveys conducted by different observers on the same plot in different years should be made cautiously.

The generality of these results is unknown and will vary. This paper indicates a method for the evaluation of these and other sources of bias in the WBPS.

ACKNOWLEDGMENTS

I am indebted to the ornithologists who helped conduct the surveys used here: G. Fairfield, D. Knauber, and D. Burton. J. Theberge provided encouragement and critical comment on the manuscript. Critical comment was also contributed by R. I. C. Hansell, J. D. Rising, A. Gotfryd, J. Root, and B. A. Maurer. The James L. Baillie Memorial Fund and the Faculty of Enviornmental Studies supplied computing funds. The Toronto Bird Observatory provided helpful support for the field studies.

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Appendix
Survey Results by Three Different Observers

Variable	Observer		
	DK	GF	PS
Mallard (*Anas platyrhynchos*)	—	0.3	1.6
Red-tailed Hawk (*Buteo jamaicensis*)	0.7[a]	0.6	—
Rock Dove (*Columba livia*)	—	0.1	—
Mourning Dove (*Zenaida macroura*)	3.7	11.5	17.4
Screech Owl (*Otus asio*)	—	0.8	—
Pileated Woodpecker (*Dryocopus pileatus*)	—	0.1	—
Hairy Woodpecker (*Picoides villosus*)	0.3	0.5	0.2
Downy Woodpecker (*P. pubescens*)	2.5	1.9	3.8
Blue Jay (*Cyanocitta cristata*)	0.5	1.0	0.6
Common Crow (*Corvus brachyrynchos*)	2.8	1.5	3.4
Black-capped Chickadee (*Parus atricapillus*)	11.5	8.4	5.0
White-breasted Nuthatch (*Sitta carolinensis*)	4.5	3.2	3.6
Red-breasted Nuthatch (*S. canadensis*)	—	0.4	0.6
American Robin (*Turdus migratorius*)	1.2	2.7	4.0
Cedar Waxwing (*Bombycilla cedrorum*)	4.2	0.1	0.2
European Starling (*Sturnus vulgaris*)	0.8	4.1	4.4
House Sparrow (*Passer domesticus*)	1.5	0.3	—
Northern Cardinal (*Cardinalis cardinalis*)	2.5	3.6	4.0
Common Redpoll (*Carduelis flammea*)	0.6	2.1	0.4
Pine Siskin (*C. pinus*)	5.0	6.0	2.8
American Goldfinch (*C. tristis*)	4.2	0.5	4.6
Dark-eyed Junco (*Junco hyemalis*)	8.7	9.9	11.6
White-throated Sparrow (*Zonotrichia albicollis*)	0.2	0.6	0.2
Song Sparrow (*Melospiza melodia*)	0.3	—	—
Total no. birds per survey	56.5	60.3	68.4
Diversity			
No. species per survey	10.8	13.0	11.4
N_2	11.16	9.69	8.95
H'	2.698	2.553	2.465
$E(S_{15})$	7.22	7.36	7.19
Evenness			
$F_{2,1}$	0.6914	0.7243	0.6947
$E_{2,1}$	0.7809	0.7962	0.8590
Number of surveys	6	10	5

[a] Values represent mean number of each species detected per count.

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RAINFALL CORRELATES OF BIRD POPULATION FLUCTUATIONS IN A PUERTO RICAN DRY FOREST: A NINE YEAR STUDY

JOHN FAABORG, WAYNE J. ARENDT, AND MARK S. KAISER

Long-term studies on the population dynamics of Neotropical bird communities have been primarily limited to Panama (see Karr et al. [1982] for a mainland site and Willis [1974] for Barro Colorado Island). An earlier paper (Faaborg 1982a) contained the first long-term population measurements from a West Indian island, specifically a seasonally-dry forest site in southwest Puerto Rico. This 5-year study apparently spanned a population peak followed by drought conditions and a severe population decline. The effects of drought on total populations, membership in different foraging guilds, and winter resident densities were discussed.

We have continued these studies and here report on 9 years of banding and population monitoring activities in a single location. This allows us to expand our previous observations on relationships between rainfall patterns and population traits of guilds and species and expose the data to statistical analyses. We also document the attempted invasion of a new species (*Elaenia martinica*) into the Guanica Forest bird community. The possible meaning of these observations in terms of island equilibrium theory (MacArthur and Wilson 1967), long-term climatic patterns (Pregill and Olson 1981), and community structure studies (Faaborg 1982b) is discussed.

STUDY AREA AND METHODS

This study was done in seasonally dry scrub in the Guanica Forest of southwestern Puerto Rico (see Terborgh and Faaborg [1973] for detailed habitat description with photographs). This habitat occurs on a coraline limestone and contains sclerophyllous forest typical of such sites throughout the West Indies (Beard 1949).

Bird population characteristics were determined by mist netting as described earlier (Terborgh and Faaborg 1973). Here we report the results of a single line of 16 mist nets (each 12 m long and 2.6 m high, 36-mm mesh, NEBBA type ATX) placed contiguously and operated from dawn to dusk for 3 consecutive days. While regressions of capture rates can be used to predict total captures, here we use simple 3-day totals. In 1976 only 2 days of netting were completed. Since the third day of netting usually yields about 20% of the total captures (range 14.7%–23.4%), we have multiplied the birds caught in 2 days by 1.25 to get the 1976 totals. Faaborg (1982a) earlier reported on the results of two separate lines, but drought at the initial location turned three small clearings into large clearings. The line considered here was operated from 1973–1983 except for 1977 and 1979. Netting (sampling) was done from early January to early February. Captured birds were banded, measured, and released, with age and sex recorded when determined. Total number for a sample

includes only the first capture of an individual in a sampling period. Recaptures are birds caught in one year but originally banded in a previous year. Bird nomenclature follows the A.O.U. Check-list (1983); common names are in the appendix.

Guild designations used are: gleaning insectivore, flycatching insectivore, nectarivore, and frugivore. (See Faaborg [1984] for a detailed rationale for these categories.) Although nearly all West Indian birds belong clearly to one of these guilds as adults, the extent that nectarivores or frugivores feed insects to their young affects our conclusions.

Because rainfall varies locally in southwestern Puerto Rico, we have used rainfall data from U.S. Weather Bureau stations at three sites surrounding Guanica. The Ensenada site is 6.4 km west of the study area, the Central San Francisco site 5 km east, and the Santa Rita site about 10 km northeast. Actual rainfall values reported in this study for Guanica were averaged across these three weather stations. Normal monthly rainfall values used were long-term averages as shown in Calvesbert (1970), and these values were also averaged across the three sites to provide normal rainfall values for the area. All precipitation variables reported as departures from normal (DFN) were calculated by comparing these representative actual and normal rainfalls in absolute values. The effect of DFN is essentially to rescale the data, based on the assumption that for bird populations adapted to a set of climatic conditions, the use of 10 for both a dry or wet year and 0 for a normal year might yield better correlations than using the actual rainfall measures. Thus, while we might expect positive correlations beween bird numbers and rainfall, we would expect negative correlations between bird numbers and DFN.

Spearman rank correlations were used to investigate the relationships between bird population levels and precipitation variables. *P*-values, the probability of obtaining a rank correlation coefficient at least as extreme as that actually observed if there is no association between the variables, are reported for all tests.

We chose several rainfall variables for correlation with the bird population data. We felt this necessary because of the highly seasonal nature of normal rainfall in the Guanica Forest (Fig. 1) and the observation that the majority of Greater Antillean birds of dry forest breed during the April–July period (Bond 1943, Diamond 1973, pers. obs.). Thus, breeding success for a year may be more closely associated with the occurrence and size of April–May rainfall than total yearly rainfall, much of which is accumulated during September and October (Faaborg 1982a). Total yearling rainfall undoubtedly affects vegetation growth and thus resource abundance for birds, but its effects may be both delayed and diffuse. Based on this rationale, we computed yearly rainfall totals both for the first 6-month period of the year (January–June) and the complete calendar year. Correlations were run between the bird population levels of a particular calendar year and total rainfall, DFN of total rainfall, 6-month rainfall, and DFN of 6-month rainfall for the current year, the previous year, the year 2 years previous, and the sum of the 2 previous years. Because of the large number of correlations computed from this data set, the probability of finding at least one significant correlation is fairly high. Thus, it is not simply the presence of a significant correlation that is important, but also the patterns of correlation between certain types of precipitation variables and the different bird guilds. In addition, we calculated correlations between bird populations sampled in January with rainfall occurring after the sample (i.e., rainfall in the current year) to test for spurious correlations; since none occurred these data are omitted here.

RESULTS AND DISCUSSION

Rainfall correlates of population variation.—Total rainfall varied rather widely through the study period (Fig. 2), while 6-month rainfall was well

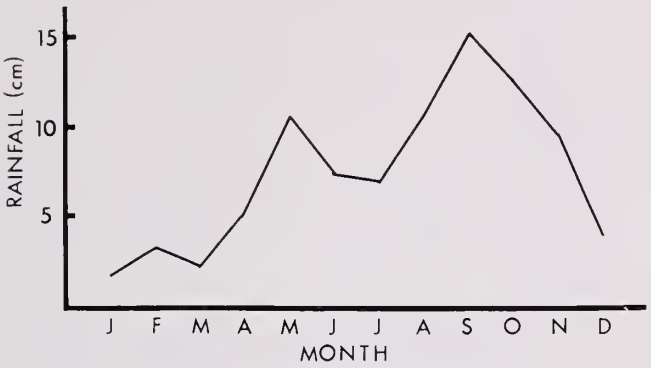

FIG. 1. Seasonal distribution of rainfall for the Guanica Forest taken as the average of the monthly averages of three nearby weather stations (Central San Francisco, Ensenada, and Santa Rita). Data are from Calvesbert (1970).

below normal from 1973–1978, but normal or above the rest of the time. The total number of resident birds captured generally was low during the middle of the sampling period with peaks in 1973 and 1982 (Fig. 3). The total number of winter resident birds did not vary as much over the years, although comparing their numbers with total resident captures obscures possibly important interactions (see below).

Dividing the resident population totals by guild membership shows varying patterns within these ecological groups (Fig. 4). Frugivore populations fluctuated substantially, with several high and low points during the study period. Nectarivores (primarily *Coereba flaveola*) declined sharply during 1974–1976 and have recovered only in recent years. The lowest capture rates for these guilds amount to less than one-third of the totals during peak years. In contrast, the relatively less abundant insectivores varied less dramatically in numbers. Gleaning insectivores showed fluctuations in numbers similar to those of frugivores but with relatively less variability, whereas flycatchers showed generally similar patterns each year with the exception of a population peak in 1976.

Most significant or near significant correlations were shown for bird populations and various measures of the rainfall occurring during the first 6 months of the year (Table 1). The single most important rainfall variable was the 6-month DFN from the previous year, which had one significant correlation (total birds, $r = -0.81$) and two strong trends: total insectivores ($r = -0.62$), and gleaning insectivores ($r = -0.61$). Two weaker trends were also shown for frugivores and nectarivores. The compound effects of low 6-month rainfall seem to be suggested by significant cor-

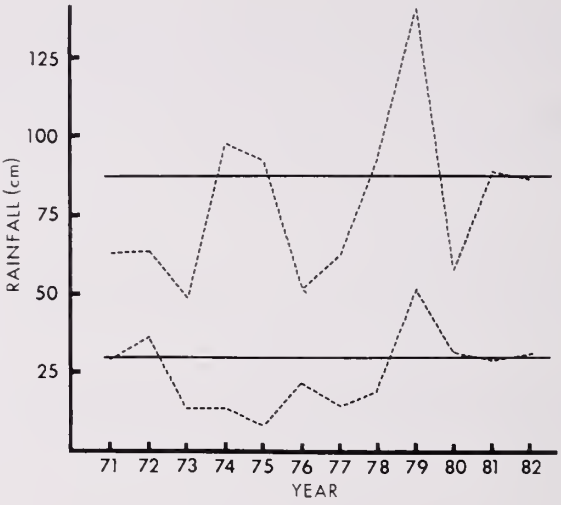

FIG. 2. Distribution of total yearly rainfall (top) and 6-month rainfall (January through June, bottom) for the period of study and two preceding years. Average values are shown as the solid flat lines. Data are averaged for the three stations as in Fig. 1.

relations between bird populations and (1) 6-month rains for 2 years previous to the sample (DFN), and (2) the sum of the 6-month rains during the 2 years previous to the birds sample (DFN). Total yearly rainfall showed no significant correlations with bird populations, although trends for the nectarivore guild and the sum of 2 previous years rainfall ($r = -0.60$) were demonstrated. However, three nearly significant correlations occur between total rainfall of the previous year and various categories

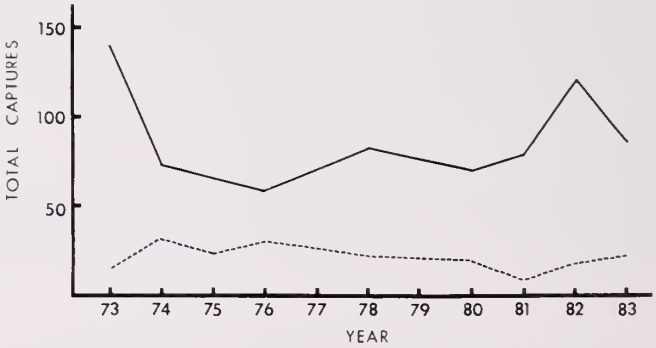

FIG. 3. Variation in the summer resident (solid line) and winter resident (dashed line) birds captured in the sampling periods during the period 1973–1983.

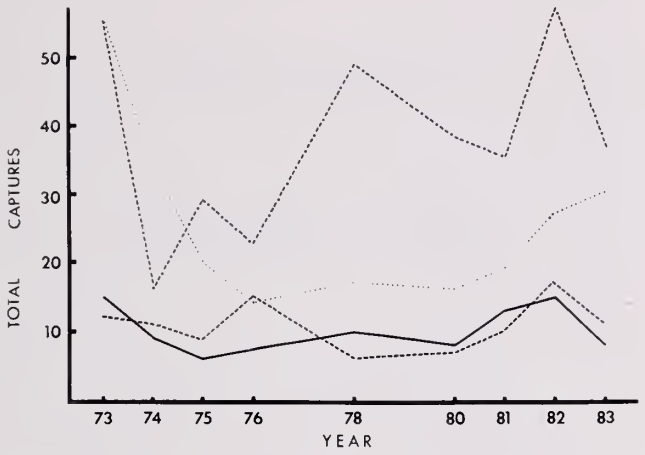

FIG. 4. Variation in captures by guild during the study. Frugivores are represented by dots and dashes, nectarivores by dots, gleaning insectivores by solid lines, and flycatching insectivores by dashes.

of insectivorous birds. The absence of a statistical relationship between yearly rainfall and bird populations may be a product of the variability (in both directions) of this rain and the fact that it is somewhat removed from directly effecting breeding success. It is apparent from these tests that Guanica Forest bird populations are very sensitive to the rainfall that ends the dry season at the start of their normal breeding period. Before we discuss this more fully, let us look at each guild in more detail.

Frugivores are notable for marked fluctuations in numbers. Earlier Faaborg and Terborgh (1980), and Faaborg (1982a) suggested that this may reflect the fact that harvesters of primary productivity face an immediate hardship with the onset of drought and cessation of production of seeds. Once those seeds on the ground are gone, food shortage may become limiting. Yet, seed production begins shortly after the rains start and the possibility for rapid population growth exists. Such a rapid population increase could occur because in the West Indies frugivores seem to have larger clutch-sizes than insectivores (Bond 1943). The only possible relationship between rainfall and frugivore numbers was a nonsignificant trend with 6-month rains for the previous year ($r = 0.62$). While this suggests frugivore dependence on April–May rains preceding their main breeding season, in several cases frugivore densities went up in years with low 6-month rainfall but high yearly rain (Fig. 5). There is some evidence (Bond 1943, Diamond 1973) that at least some West Indian frugivores may breed into August or September, although the situation

TABLE 1

P-VALUES FOR SPEARMAN RANK CORRELATIONS BETWEEN BIRD POPULATION LEVELS AND PRECIPITATION VARIABLES

Precipitation variable	Total birds	Frugivores	All insectivores	Gleaning insectivores	Flycatching insectivores	Nectarivores
Total, 1 year previous	0.2867	0.7324	0.1447	0.1407	0.9145	0.2054
Total, 1 year previous, DFN	0.4879	0.6059	0.5003	0.8291	0.1145	0.6682
6 month, 1 year previous	0.1705	0.0769	0.6989	0.2176	0.6816	0.7001
6 month, 1 year previous, DFN	0.0079*	0.1098	0.0738	0.0757	0.4751	0.1447
Total, 2 years previous	0.5165	0.3807	0.7640	0.7787	0.7466	0.3807
Total, 2 years previous, DFN	0.8984	0.8312	0.6989	0.3617	0.5874	0.9661
Six month, 2 years previous	0.1116	0.7324	0.0091*	0.0176*	0.4154	0.1544
Six month, 2 years previous, DFN	0.0159*	0.1544	0.1854	0.2081	0.2011	0.0358*
Total, sum of 2 previous years	0.2861	0.8312	0.4308	0.3251	0.7139	0.0876
Total, sum of 2 previous years, DFN	0.8984	0.7650	0.8305	0.4541	0.4288	0.7001
6 month, sum of 2 previous years	0.1875	0.2242	0.2624	0.0773	0.9829	0.5755
6 month, sum of 2 previous years, DFN	0.0159*	0.1116	0.1524	0.1561	0.3515	0.0769

* Significant at $P \leq 0.05$.

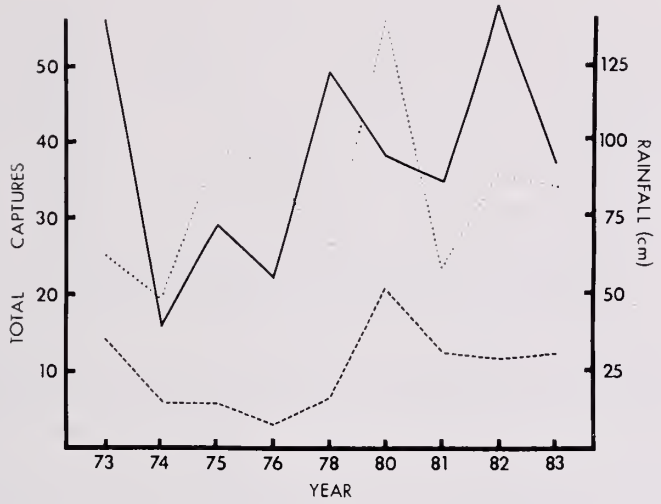

FIG. 5. Variation in the number of frugivores captured in each sample (solid line), total yearly rainfall for the calendar year preceding the sample (dotted line) and 6-month rainfall for the year preceding the sample (dashed line).

at Guanica vis-a-vis these species is unknown. Such an extended breeding season would allow frugivores to take advantage of more predictable late-season rains.

Resident insectivores (including both gleaners and flycatchers) did not show sharp fluctuations from year to year (Fig. 6). With the exception of a 1976 increase caused solely by an unusually large number of *Myiarchus antillarum,* resident insectivore numbers declined in 1974 and 1975 and remained low until increasing in 1981–1982. This pattern is not quite significantly correlated with the DFN for the first 6 months of the year previous to the sample ($r = -0.62$), but is significantly correlated with 6-month rain 2 years previous to sampling ($r = 0.80$). The numbers of gleaning insectivores showed the same general relationship plus one strong trend for the 6-month sum of the 2 previous years ($r = 0.61$). Flycatchers showed no significant correlations with rainfall and only one general trend thereto (DFN of total rain in previous year). The 1983 decrease in insectivorous birds did not correspond to the rainfall totals, probably because most of the 1982 rain fell in one downpour that was mostly lost to runoff (B. Cintron, pers. comm.). Population responses to changing climatic conditions seem to show a lag for insectivores, which may reflect the fact that insects have life cycles of their own and thus are a somewhat buffered resource for birds to use (Faaborg and Terborgh 1980, Faaborg 1982a). In addition, clutch-sizes of insectivores are generally small and,

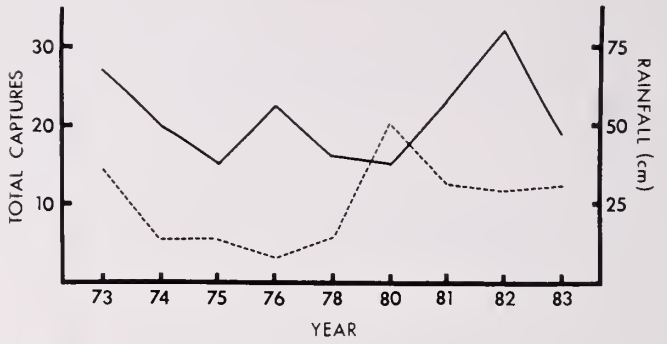

FIG. 6. Variation in the number of resident insectivores (both gleaners and flycatchers) captured (solid line) and 6-month rainfall for the period preceding the sample (dashed line).

as noted earlier, insectivorous species of birds appear to be restricted in Guanica to breeding during a few months. Thus, while wet season rains undoubtedly aid survivorship, the success of insectivore reproduction seems to be mostly dependent upon the length of the dry season and the occurrence of an adequate April–May rainy season.

Assessment of the effects of dry conditions on resident nectarivores in the Guanica Forest is based primarily on *Coereba flaveola*. The only common hummingbird (*Anthracothorax dominicus*) seemingly declined in numbers early in the study period and was not caught at all in 3 of the last 5 sampling years. No more than five individuals of this hummingbird were captured in any year. *Coereba* declined dramatically in the 1974–1976 interval, then leveled off until an increase in numbers began in 1981 (Fig. 4). A significant correlation occurred between nectarivore numbers and rainfall for one 6-month value (DFN of 2 years previous, $r = -0.70$) and trends occurred for summed DFN of the previous 2 years ($r = -0.62$) and the sum of the 2 previous years total rainfall ($r = 0.60$). The pattern for nectarivores resembles that of the insectivores except for a seemingly delayed response to rainfall and greater variation in numbers (*Coereba* alone nearly equaled the frugivores in 1973). Such variation in numbers is perhaps to be expected for a generalist like *Coereba,* which, in addition to nectar, takes soft fruits and gleans insects. Our observations and the absence of both fruits and flowers suggest that *Coereba* was primarily an insect gleaner during the aforementioned drought. While this species has been recorded breeding in all months of the year in other parts of Puerto Rico, we have never seen it breeding in winter in Guanica. A somewhat restricted breeding season may explain *Coereba*'s slow population increase, while its diverse diet may allow it to achieve high densities when conditions are favorable.

Thus, in the seasonal conditions of the Guanica Forest, the occurrence and size of early wet season rains is seemingly correlated with population sizes of all avian guilds. Since these rains follow a 4-month long dry season, they are critical to the nesting success of birds that breed during the April–July period. The question that arises at this point is: Given a more predictable August–November wet season, why do most, if not all, species confine their breeding to the April–July period? There is some evidence that arthropods are plentiful at this time (Kepler 1972, Diamond 1973, Janzen 1973), although these studies were based on the use of a variety of techniques of resource assessment applied in different habitat types. Any increase in insect numbers depends upon the rains which signal the beginning of the wet season, thus, in terms of resource availability it is less apparent why birds don't initiate breeding in August or September if rains are delayed until then. We believe that another important factor relates to the presence of high densities of winter residents that are primarily insectivores, including some which flycatch (Bennett 1980). These wintering migrants may be sufficiently numerous to have effects upon resident insectivores and, to the extent that these birds feed their young insects, even frugivores and nectarivores.

While Fig. 3 shows that winter resident numbers did not fluctuate as greatly as those of permanently resident species, a closer look at winter resident numbers and resident insectivore (including *Coereba*) totals, shows the potential for interaction among these groups (Fig. 7). In many years, the number of winter resident insectivores exceeds that of resident gleaners and flycatchers, a fact that at the least must affect the breeding season of Guanica's warbler and vireo, if not other species. Although no statistical correlations between the numbers of these groups were found, in several cases an increase by one group has been accompanied by a decrease in the other, suggesting some sort of competitive interaction. While a detailed discussion of interactions among the insectivores and *Coereba* is difficult without some measure of the effects of drought on insect numbers, we can look at how the total number of insectivores varied over the study to get some idea of habitat carrying capacity for insectivores. This density was at its peak in 1973 (although many of *Coereba* at this time must have been highly nectarivorous), occurring after at least two wet breeding seasons, even though those 2 years had below-normal yearly rainfalls. The lowest insectivore totals occurred in 1980 and 1981, even though 1979 was one of the wettest years in the study, both before and after July. This lag in the recovery of insectivore populations may well reflect a lag in population growth of insects following the end of the drought, coupled with the effects of small clutch-size and limited breeding season in Guanica birds.

While it is perhaps not surprising that all resident and winter resident

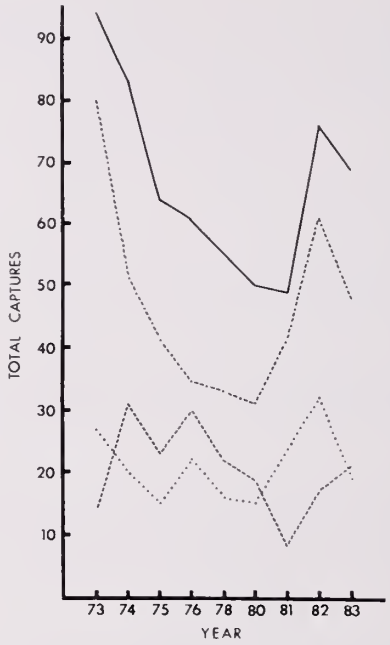

FIG. 7. Variation in insectivores captured throughout the study. The dashed line shows winter resident numbers, the dotted line resident insectivores (gleaners and flycatchers), the dash-dot line resident insectivores plus *Coereba*, and the solid line all insectivores (residents and winter residents).

insectivores reached their lowest levels at the same time, the fluctuations of these groups before this sharp reduction in numbers are of interest. Except for the drought, winter residents showed lowest densities when resident insectivores had their highest, and as the drought caused resident insectivore numbers to decline, winter resident populations actually climbed and stayed high until resource limitation apparently occurred. The winter residents have the advantages of using the Guanica Forest only for survival during their winter tenure, obtained by arriving during the more resource stable season, and by having more flexibility in choice of specific sites at which to winter. We suggest that when resident insectivore numbers are reduced due to a dry breeding season, winter residents can respond to the decrease by increasing their numbers to the extent made possible by rainy season conditions. In contrast, when resident insectivore populations are high, in turn they may limit the number of winter residents in the Guanica Forest. The specific traits of these winter residents are discussed elsewhere (Faaborg and Arendt 1984); suffice to

say we see two types of winter residents. One type is present in the Guanica Forest each winter and generally shows a high degree of wintering philopatry; populations of these vary somewhat but do not correspond to any of the weather patterns. A second set of warblers, seemingly much more opportunistic, was more abundant when resident numbers were low. The Cape May (*Dendroica tigrina*) and Prothonotary (*Protonotaria citreria*) warblers were found only when resident numbers were low while the American Parula (*Parula americana*) and Prairie Warbler (*Dendroica discolor*) were commonest at this time.

Certainly more data on bird and resource populations are needed to understand any effects of competition in this situation. Assessing competition is complicated by the need to intepret import of several species that occur in the Greater Antilles only during the breeding season (Faaborg and Terborgh 1980). Perhaps as well as any other, this situation exemplifies the complexity of potential competitive interactions and the fact that they do not always involve simple exclusions or the responses to "ecological crunches." In this case, one set of competitors (winter residents) seems to restrict the other set (resident insectivores) to a relatively short breeding season. Whether or not the winter residents "win" is seemingly a function of the climatic conditions at the time the residents breed. Thus, a critical determinant of the outcome of a competitive interaction occurs when the competing groups are thousands of miles apart. The extent that frugivores feed their young insects adds to the complexity of this situation; we hope to study this in more detail in the future.

Species responses to drought.—The decline of captures of a species may reflect actual mortality of local residents, movement from the sampling area, or net shyness of birds previously captured. Because our net samples were a year apart, often included a high percentage of recaptures, and showed some of the lowest totals after 2-year intervals, we doubt that net-shyness is of great importance. Looking at the fluctuations of each species through this 10-year period, along with measurements on the rate of recapture of banded birds and measurements of longevity (Table 2) gives us some idea of the range of strategies used by individual species to survive these conditions. It should be noted that the highest rate of recapture of all individuals (the proportion of birds in a sample banded in previous studies) was about 50%, suggesting a fairly high rate of local turnover at all times.

As the most complex guild, it is not surprising that frugivores show the greatest variety of responses to drought conditions. With the exception of the large doves that are not easily captured, *Euphonia musica,* an erratic wanderer that feeds on mistletoe, and *Spindalis zena,* none of the frugivores was ever absent for more than two sampling periods and all pop-

TABLE 2

INFORMATION ON RECAPTURES OF GUANICA FOREST BIRDS BETWEEN SAMPLING PERIODS

Species	Total captures[a]	No. recaptures	Mean duration[b]	Longest[c]
Columbina passerina	41	2	1, 6	2, 0
Todus mexicanus	26	4	4, 6	8, 11
Melanerpes portoricensis	7	1	1, 0	1, 0
Myiarchus antillarum	50	14	3, 3	9, 6
Elaenia martinica	18	4	1, 3	1, 11
Margarops fuscatus	74	9	2, 8	6, 0
Turdus plumbeus	39	11	2, 10	6, 6
Vireo latimeri	18	6	1, 9	4, 1
Dendroica adelaidae	45	10	2, 9	7, 0
Coereba flaveola	242	31	2, 0	5, 0
Spindalis zena	18	1	1, 0	1, 0
Icterus dominicensis	4	2	1, 6	2, 0
I. icterus	14	1	2, 0	2, 0
Loxigilla portoricensis	131	18	1, 5	3, 0

[a] Number of new captures in each sample summed for the nine samples.
[b] In years, months.
[c] Longest time between recaptures.

ulations increased with the amelioration of "unfavorable" conditions. The smaller frugivores showed the greatest fluctuations. *Columbina passerina* dropped from 16 captures to 1 capture in just a year and has been of spotty occurrence in recent years; *Tiaris bicolor* dropped from six to zero individuals during the same period. Both of these species prefer clearings for feeding and appear to be the most nomadic of the frugivores, as we recaptured no grassquits and just 2 of 41 ground doves (Table 2). *Loxigilla portoricensis* also declined dramatically (from 22–6 captures) but it showed a 14% recapture rate overall and 37% rate at the lowest population levels.

The two large but common frugivores fluctuated less than the small species and actually increased during and following the severest drought period. *Margarops fuscatus* showed a 12% recapture rate overall, with most of the recaptures late in the study when the numbers of this species had increased. Although *Turdus plumbeus* was not netted in the abbreviated 1976 sample, it too generally showed no decline during the drought and an early increase after it. Both species had long-lived individuals, with thrushes recaptured at up to 6.5-year intervals. The apparent immunity of these larger frugivores to severe conditions is in accord with arguments suggesting they have higher survival capacities than small birds on islands (Grant 1968, Wilson 1975), perhaps because they feed on more animal matter (either insects or lizards) than the other frugivores.

Two nectarivores showed distinct declines during the drought. *Anthra-*

cothorax dominicus declined from a high of three individuals to two in 1976, then was captured again only once until 1983. *Coereba* dropped from 53–11 captures in a 3-year period and was seemingly fairly sedentary, with a 13% recapture rate overall and yearly rate up to 38% during the decline. The oldest recapture for this species was 5 years with a mean recapture time of 2 years.

Only four resident insectivores could be effectively sampled by nets throughout the study. *Tyrannus dominicensis* was common but stayed above the canopy at Guanica, while the cuckoos were both uncommon and large enough that netting was a poor sampling tool. All the nettable insectivores showed declines. *Myiarchus antillarum* fluctuated between 11 and 2 individuals, while the tiny flycatching *Todus mexicanus* ranged from one to six individuals. Both of these species showed high overall recapture rates and both have longevity records approaching 10 years (8.9 years for the tody and 9.5 years for the flycatcher). The two small permanent resident gleaners include *Dendroica adelaidae* which varied from one to eight individuals and *Vireo latimeri* which ranged from four to zero captures. *Dendroica* showed a 22% overall recapture rate while *Vireo* had a 33% rate; both had individuals that lived through much of the drought. The Black-whiskered Vireo (*Vireo altiloquus*) breeds at Guanica but has never been captured in the dry season because it winters in South America.

While we did not catch a few species in some samples, in all cases these species were observed in the Guanica Forest area during the sampling period. Only the hummingbird and *Spindalis* (which may not breed at Guanica) were not seen somewhere in the forest each sampling period. While a few species seemed to be somewhat nomadic on a local scale, most appeared fairly sedentary. A preliminary analysis of our weight measurements (Arendt and Faaborg, unpubl.) has shown no changes in mean weights during the drought, suggesting that maintenance of adult birds may not be as difficult as successful reproduction seems to be. All the species seemed well-adapted to exceptionally harsh conditions in an always harsh environment.

The attempted invasion of the Caribbean Elaenia.—Although none of the species present before the onset of drought disappeared from Guanica, an apparent temporary invasion of the Caribbean Elaenia into this area did occur. This species was not recorded in the forest until an individual was captured in the initial netline in 1975, after at least 1000 individuals of other species had been netted. No additional elaenias were netted until 1980. Then the capture rate increased to six in 1981 and nine in 1982, of which three were recaptures. Only two, however, were netted in 1983, one of these a recapture from 1981.

Although the Tyrannidae are generally thought of as insectivores, *Elaen-*

ia spp. are well known for their fruit-eating preferences (Crowell 1968). Nonetheless *E. martinica* regularly hawks insects; Faaborg (unpubl.) found its insectivorous habits to predominate during the drought of 1973 on Vieques Island. In assigning guilds, we attemped to go by the foods or feeding technique critical to a species during stress periods. For this reason we grouped *Elaenia* with the other flycatchers, many of which eat fruit when it is available.

The range of *E. martinica* in the West Indies suggests that it could be categorized as a "tramp" following Diamond (1975). It is found from Aruba, Providencia, and St. Andrews, northward throughout the Lesser Antilles and islands east of Puerto Rico, and on the Cayman Islands, the only place where it coexists with a similar-sized tyrannid. (Johnston [1975] felt this coexistence was possible because *Elaenia* ate so much fruit, but that explanation does not seem to apply elsewhere.) It is only patchily distributed on Puerto Rico and absent from the other Greater Antilles. The combined characteristics of wide range but absence on larger islands with higher species numbers fit the tramp designation perfectly. Following the logic of Diamond (1975), we can look at this species as one that is a poor competitor that cannot survive on large islands but an excellent disperser and generalist that excels on small islands.

If true, how will these traits affect *E. martinica*'s chances of becoming permanently established in the Guanica Forest bird community—one of the most complex in the Caribbean? First, it should be noted that *E. martinica* is about the size of the resident flycatcher (*Myiarchus antillarum*). Only on the Cayman Islands do two like-sized flycatchers coexist, so this appears to be an unstable situation in which competitive exclusion of one or the other species may occur. *Myiarchus* sp. and *Elaenia* sp. do coexist on some Lesser Antillean islands, but on these islands the large *Myiarchus* sp. is usually not found with a large (45 g) kingbird (*Tyrannus* sp.), as is the case at Guanica. There *Myiarchus* may have an advantage as an established resident, but in turn the broader diet of *E. martinica* may be of advantage to it. It should be noted again that *Elaenia* appeared and increased at the time of general increase in most populations following cessation of the drought. This would have been a period when food levels were relatively high while competitors were few, a seemingly excellent time for an "invasion" attempt. The overall decline in populations found in 1983 was particularly hard on this species, perhaps because resources had once again become limited and competition was having its effects. Should *E. martinica* ultimately be excluded, it would lend support to the contention that it is a poorly competing tramp species using an "in-and-out" strategy of attempted colonization.

Saturation and stability in the Guanica Forest bird community.—The

overriding conclusion from our data seems to be that the Guanica Forest supports a set of resident species which can coexist during severe drought conditions without any loss of species. While many species reached low levels in our net samples, they were widespread throughout the forest and did not face threat of extinction. Perhaps a competition among these species in the drought and in previous "ecological crunches" (Wiens 1977) has led to the fairly simple and conservative patterns of structure we find in West Indian bird communities (Terborgh and Faaborg 1980; Faaborg 1982b, 1984). In as much as colonization rates are very low on these islands, intervals are not long enough between stress periods for high turnover of species. Thus, the apparent results of competition in determining the component species on these islands are everpresent, while actual species densities may fluctuate somewhat independently in response to the specific resources available to a species. Pregill and Olson (1981) pointed out that dry forest vegetation such as that found at Guanica was much more common in the West Indies during Pleistocene dry periods; thus, we may be seeing super-saturated communities in this habitat today. While we think their observation is important in explaining the difference in species densities between wet and dry forests in the West Indies today, the observed stability of this community through severe conditions suggests it is quite resistant collectively to extinction. On the other hand, the difficulty that *E. martinica* appears to be having and the fact that none of the many introduced species common in Puerto Rico (Raffaele 1983) has been seen in the forest suggests that the Guanica Forest bird community is resistant to the successful invasion of new species.

SUMMARY

Possible interactions between bird population fluctuations and rainfall patterns are discussed using data gathered over 9 years in the period 1973–1983 (no netting was done in 1977 or 1979) in a Puerto Rican dry forest. Bird populations were assayed using a 16-net line of mist nets operated from dawn to dark for 3 consecutive days in January or early February of each year. Total captures were divided by resident or winter resident status and the residents divided into four guilds based on foods and/or foraging behavior. The rainfall data used were an average of measurements from three weather stations within 10 km of the study site. Average monthly rainfall at these sites was added both for yearly totals and for a 6-month total covering the period January–June, a potentially critical value as April and May rains seem to be necessary to end the effects of the dry season at the start of the normal April–July bird breeding season. Spearman rank correlations were used to assess the relationships between bird population levels and precipitation variables.

Total yearly rainfall varied widely throughout the study while 6-month rain totals were below normal for the period 1973–1978. Total bird populations peaked in 1973 and 1982 and were lowest in 1976. Virtually all the significant correlations that occurred were between bird population levels and measures of the 6-month rainfall. It is suggested that without ample totals from these rains, local birds cannot successfully rear young during their normal April–July breeding period. We further suggest that the resident birds do not delay their

breeding season until the more predictable rains of August–November because of the relatively large influx of winter resident insectivores that appear at this time. Winter resident densities often exceed those of resident insectivores, a fact which must affect selection for resident insectivore breeding seasons and would affect frugivores to the extent that the latter feed insects to their young.

Some further possible interactions between resident and non-resident birds are discussed. Some of the characteristics of longevity and site-fidelity of the resident species are described. Also documented is the invasion of the Caribbean Elaenia (*Elaenia martinica*), a species not recorded in Guanica Forest until 1980, whose numbers peaked in 1982, and now has apparently only a tenuous hold within the study area. The facts that no species was extirpated during the severe drought and neither *E. martinica* or any introduced species have successfully colonized the Guanica Forest community suggest it is at equilibrium.

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Appendix

Number of New Captures of Individuals of Each Species during Each Sampling Period

Species	1973	1974	1975	1976[a]	1978	1980	1981	1982	1983
Frugivores									
Zenaida Dove (*Zenaida aurita*)	—	—	—	—	1	—	—	—	—
Common Ground Dove (*Columbina passerina*)	16	1	7	4	6	—	4	—	3
Key West Quail-dove (*Geotrygon chrysia*)	—	—	—	—	2	1	—	—	1
Pearly-eyed Thrasher (*Margarops fuscatus*)	4	5	8	5	11	8	8	16	9
Red-legged Thrush (*Turdus plumbeus*)	2	2	5	—	4	10	5	6	6
Antillean Euphonia (*Euphonia musica*)	—	—	—	1	—	—	—	—	—
Stripe-headed Tanager (*Spindalis zena*)	6	2	1	—	1	2	1	5	—
Puerto Rican Bullfinch (*Loxigilla portoricensis*)	22	6	8	6	18	13	16	29	13
Yellow-faced Grassquit (*Tiaris olivacea*)	—	—	—	1	—	—	—	—	—
Black-faced Grassquit (*Tiaris bicolor*)	6	—	—	1	6	4	1	2	5
Gleaning Insectivores									
Mangrove Cuckoo (*Coccyzus minor*)	—	—	—	—	—	2	—	1	—
Puerto Rican Lizard-cuckoo (*Saurothera vieilloti*)	1	—	—	1	—	1	2	1	—
Puerto Rican Vireo (*Vireo latimeri*)	4	2	1	—	2	2	4	3	—
Adelaide's Warbler (*Dendroica adelaidae*)	5	6	1	1	7	3	7	8	7
Black-cowled Oriole (*Icterus dominicensis*)	1	1	2	—	—	—	—	—	—
Troupial (*Icterus icterus*)	4	—	2	4	1	—	—	2	1
Nectarivores									
Antillean Mango (*Anthracothorax dominicus*)	3	1	2	2	—	—	1	—	1
Bananaquit (*Coereba flaveola*)	53	33	18	9	17	16	18	27	29
Flycatching Insectivores									
Gray Kingbird (*Tyrannus dominicensis*)	—	—	—	—	1	—	—	—	—
Puerto Rican Flycatcher (*Myiarchus antillarum*)	6	5	8	11	4	2	3	5	6

Appendix
Continued

Species	1973	1974	1975	1976[a]	1978	1980	1981	1982	1983
Caribbean Elaenia (*Elaenia martinica*)	—	—	—	—	—	1	6	9	2
Puerto Rican Tody (*Todus mexicanus*)	6	6	1	1	1	4	1	3	3
Miscellaneous Species									
American Kestrel (*Falco sparverius*)	1	—	—	—	—	—	—	—	—
Puerto Rican Woodpecker (*Melanerpes portoricensis*)	—	3	—	—	—	—	1	3	—
Puerto Rican Screech-owl (*Otus nudipes*)	—	—	1	—	—	—	1	—	—
Total resident individuals	140	73	65	47	82	69	78	120	86
Total winter residents	14	31	23	24	22	19	8	17	21
Grand total captures	154	104	89	71	104	88	86	137	107

[a] Because only 2 days of netting were done, these totals were multiplied by 1.25 to get a projected total for 3 days when graphing patterns in Figs. 1–7.

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PARENTAL FEEDING OF NESTLING NASHVILLE WARBLERS: THE EFFECTS OF FOOD TYPE, BROOD-SIZE, NESTLING AGE, AND TIME OF DAY

RICHARD W. KNAPTON

About 90% of all bird species are reportedly monogamous (Wittenberger 1982). Monogamous mating systems are associated with biparental care, and one hypothesis for the evolution of such mating systems is that male help is essential to the successful rearing of young. A prediction of this hypothesis is that a male should contribute a substantial amount of food to the raising of nestlings; this was tested in an essentially monomorphic, monogamous paruline, the Nashville Warbler (*Vermivora ruficapilla*).

Relative parental contribution in terms of rates of feeding young can be influenced by demands of the nestlings (e.g., brood-size, nestling age) and/or by environmental factors (e.g., weather conditions, time of day, time of season) (Royama 1966, Willson 1966, Seel 1969, Best 1977, Pinkowski 1978, Johnson and Best 1982, Wittenberger 1982, Bèdard and Meunier 1983). Rates of feeding per se can be potentially misleading in determining relative contributions of the male and female parent if the food packages brought to the young differ in some way between the parents; a few studies (e.g., Howe 1979, Knapton 1980, Johnson and Best 1982, Biermann and Sealy 1982, Bèdard and Meunier 1983, Knapton and Falls 1983) have taken this into account in their comparisons of male and female contributions.

The objectives of this study were: (1) to document patterns of feeding nestling Nashville Warblers between members of a pair; and (2) to compare these patterns between pair members as they relate to brood-size, nestling age, and time of day. In the comparisons, I take into account not only rates of feeding but also the identity, size, and number of prey items.

METHODS

The study was carried out in Algonquin Provincial Park, Ontario, during the breeding seasons of 1981 and 1982. The habitat occupied by Nashville Warblers in the park is mixed coniferous and deciduous woodland with open areas covered with low shrubs (primarily *Vaccinium* spp.), ferns and forbs.

We located nests by systematically searching openings in the forest in three study areas. All nests were discovered when the incubating bird (in all instances, the female) was flushed from the nest. All nests when found contained eggs, and a daily log of each nest's progress was kept until it was empty, either the young fledged or the nest contents depredated. Thus, the age of the nestlings at any given time could be determined.

Adults were caught in two ways: (1) in mist nets with a playback of a Nashville Warbler's song; and (2) by butterfly net, a method which proved most effective in catching the incubating female (Knapton, unpubl.). This latter method involved approaching the nest and quickly covering it with the net. Most birds were caught on the first attempt, no bird sustained an injury from this method, and no nest was lost to desertion. Each bird caught was color-banded, for individual recognition, and sexed by presence or absence of cloacal protuberance and by slight plumage differences (females tended to be slightly duller than males). Subsequent behavioral differences (e.g., singing by males, incubating by females) confirmed these sexing methods.

Nashville Warbler nests were watched from blinds set up about 10 m away, and the parent birds were observed as they approached the nest with food in their bills, fed the nestlings, and then flew off (called a feeding trip). Most nests were watched on 5 consecutive days, from day 4–day 8 of the nestling period (the young fledged on day 9), in the period 11–26 June. Observation periods were about 3 h long, and were carried out between 08:00 and 20:00 EDT. For analysis, each day was divided into four 3-h time periods: 08:00–11:00, 11:00–14:00, 14:00–17:00, and 17:00–20:00. No observations were carried out in cool or rainy weather. Pairs appeared to accept the presence of blinds, and no nest under observation was deserted. Information was recorded on portable tape recorders and later transcribed.

From blinds, the following information was recorded: (1) the number of foraging trips; (2) the sex of the bird making the trip; (3) the number of prey items each bird brought back to the nest at each trip; (4) where possible, the identity of the prey items, at least to order and occasionally to family; and (5) the size of each prey item, to the nearest 0.5 cm, relative to bill length (8–10 mm).

In 1980, nestlings from five nests (two nests of three young, two of four young, one of five young) were weighed to the nearest 0.1 g from day 0 (day of hatching) to day 8, and growth curves constructed (Knapton and Cartar, unpubl.). Analyses of variance showed no significant differences in nestling weight at any age among different brood-sizes. Young were not weighed in 1981 and 1982 to avoid disruption of nesting activity and possible increased predation levels from observer activity.

Data were analyzed by one-way or two-way ANOVAs, or by paired *t*-tests. The degree of dietary overlap between males and females was determined using Horn's (1966) measure of overlap, C, given by the equation:

$$C = \frac{2 \sum_{i=1}^{s} X_i Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where X_i and Y_i are the proportions of prey species i for males and females, respectively. A value of 0% means no overlap, a value of 100% means total overlap.

RESULTS

Eleven nests were watched, at an average of 16.4 h/nest; 1324 foraging trips were recorded. Five nests were observed in 1981 and six in 1982; there were no differences in feeding rates between years for males (t = 0.46, NS) or for females (t = 0.64, NS), hence data for both years were pooled. Brood-size was four nestlings in six nests and five nestlings in five nests.

TABLE 1
A COMPARISON OF INTERSEXUAL FEEDING RATES IN 11 PAIRS OF NASHVILLE WARBLERS

Pair	Feeding rates (trips/h)			Brood-size
	Male	Female	Total[a]	
1	5.88	5.06	10.94	4
2	1.45	8.84	10.29	5
3	4.60	4.07	8.67	5
4	4.16	4.45	8.61	4
5	4.01	3.67	7.68	5
6	3.53	3.60	7.13	4
7	2.94	3.96	6.90	4
8	3.49	3.39	6.88	5
9	2.91	2.95	5.86	5
10	2.72	3.01	5.73	4
11	0	3.43	3.43	4

[a] Total feeding rates are arranged in decreasing frequency.

Comparison of total male and female contributions to feeding nestlings.—There was no difference between the sexes in feeding rate (Table 1: $t = 1.35$, df = 10, NS). Mean male feeding rate was 3.24 ± 1.57 trips/h, and mean female feeding rate was 4.22 ± 1.65 trips/h. The lower mean rate of feeding by males is almost entirely due to two nests at which the female contributed much more than her partner, at 85.9% at nest 2 and 100% at nest 11. At the nine other nests, males and females contributed more or less equally (Table 1: $t = 0.21$, df = 8, NS). The absence of male feeding trips at nest 11 was not because the male was not present: the male made frequent visits to the vicinity of the nest but never with food in its bill and never actually to the nest itself.

Number, size, and identity of prey delivered to young.—Number of prey items per foraging trip ranged from one to three (males: $\bar{x} = 2.01 \pm 0.51$; females: $\bar{x} = 1.78 \pm 0.34$). There was no difference between the sexes in number of prey brought to the nest; mean number of prey delivered to nestlings/h for males was 6.51 ± 1.48 and for females was 7.52 ± 1.28 ($t = 1.06$, df = 10, NS).

Prey type did not differ between the sexes; the dietary overlap value C = 94%, indicating almost complete overlap between males and females in prey type. Lepidoptera larvae comprised 89% of all prey types, the remaining 11% being made up of adult Diptera, spiders, adult Coleoptera, and an unidentified category. Lepidoptera larvae comprised 88% of male contributions and 90% of female contributions.

Prey length also did not differ between the sexes ($F = 0.94$, df = 1,60,

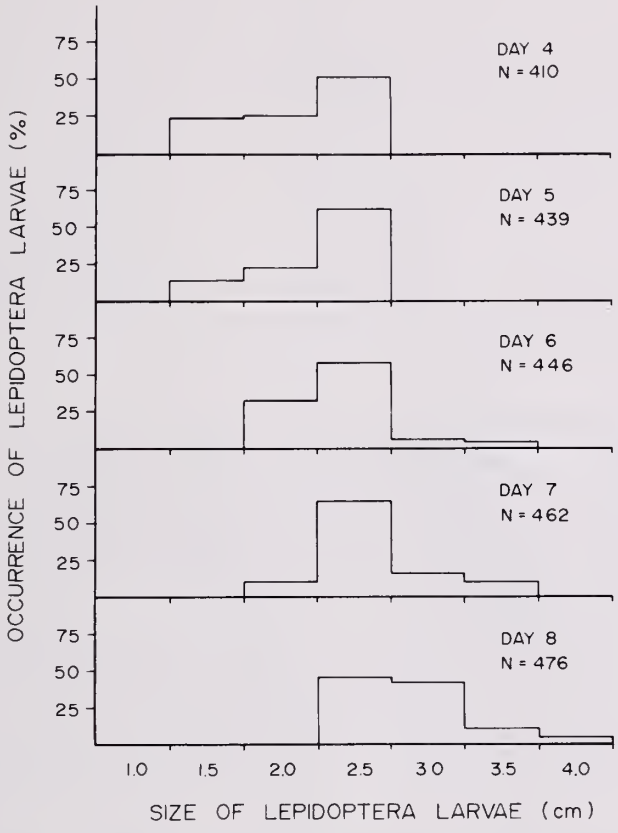

FIG. 1. Frequency distribution of Lepidoptera larvae of different sizes as a function of nestling age. N = total number of larvae per each age class.

NS). The most frequent size of Lepidoptera larvae taken was 2.5 cm long, followed in decreasing frequency by larvae at 2, 3, 1.5, 3.5, and 4 cm long, respectively (Fig. 1). However, prey size did increase with age of nestlings (see below). As a general conclusion, there was no difference between males and females in number, prey type, or size of prey delivered to nestlings.

Brood-size.—Brood-size did not affect feeding frequency ($F = 0.27$, df = 1,18, NS), and there was no brood × sex interaction ($F = 0.17$, df = 1,18, NS). Mean rates of nest visitation were as follows: males = 3.21 ± 1.94 for broods of four, and 3.28 ± 1.20 for broods of five; females = 3.92 ± 0.74 for broods of four and 4.59 ± 2.41 for broods of five.

Brood-size also did not affect feeding frequency in terms of number of

TABLE 2
MALE AND FEMALE FEEDING RATES (TRIPS/H) AND AGE OF NESTLINGS AT 11 NASHVILLE WARBLER NESTS

Age of nestlings (days)	Male ($\bar{x}$ ± SD)	Female ($\bar{x}$ ± SD)
4	2.82 ± 1.70	4.10 ± 2.71
5	3.21 ± 1.45	4.18 ± 1.50
6	3.38 ± 1.53	4.13 ± 1.18
7	3.27 ± 1.77	4.52 ± 2.47
8	3.39 ± 1.99	4.62 ± 1.96

feeding trips per nestling ($F = 0.41$, df = 1,18, NS) and once again there was no brood × sex interaction ($F = 0.07$, df = 1,18, NS).

Nestling age.—Feeding rates of either sex did not change with nestling age (males: $F = 0.73$, and females: $F = 0.51$, for each analysis, df = 4,50, NS). Feeding rates remained essentially constant over the 5-day period for both sexes (Table 2), with females averaging more feeding trips/h than males at each nestling age.

There was, however, an increase in prey size with nestling age (Fig. 1; $F = 14.24$, df = 5,20, $P < 0.001$). Lepidoptera larvae at 2.5 cm long predominated at all nestling ages, but nestlings at days 4 and 5 received proportionately more larvae 1.5 and 2 cm long; whereas, older nestlings received an increasing proportion of larvae 3–4 cm long. The increase in prey size with nestling age is probably not due to prey availability, as nestling age among nests was not synchronous. There was considerable overlap in nestling age among nests that were watched such that two nests observed on the same day could hold young at any age between 4 and 8 days old.

Time of day.—Time of day had a significant effect on feeding rates (Fig. 2, $F = 4.58$, df = 3,80, $P < 0.01$). Most feedings occurred in the early morning and evening periods for both sexes. A comparison of male and female feeding rates during the day showed a significant difference between the sexes (Fig. 2; $F = 7.35$, df = 1,80, $P < 0.01$). A general statement is that males fed comparatively less in the early morning and evening periods and more during the rest of the day than females.

DISCUSSION

Relative parental contribution is a function of feeding rates, number of prey items per feeding trip, and nature of the prey. Feeding rates per se are not necessarily a true indicator of parental contribution if aspects

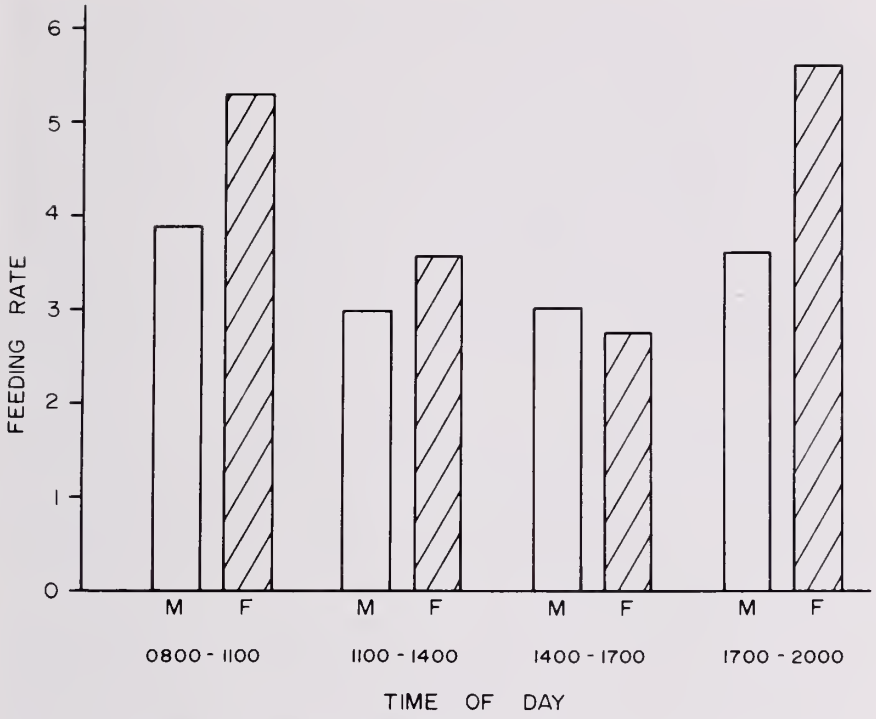

FIG. 2. Comparison of male and female feeding rate (trips/h) according to time of day.

of the prey brought in during feeding trips differ between the sexes (Royama 1966, Howe 1979, Johnson and Best 1982, Wittenberger 1982, Biermann and Sealy 1982, Bèdard and Meunier 1983).

In the Nashville Warbler, the nature of the prey (its size and identity) brought to nestlings did not differ between males and females within a pair at each of the 11 nests observed. Lepidoptera larvae were the most common prey item, with larvae 2.5 cm long being the most frequently delivered size. Number of prey items per feeding trip also did not differ between the sexes, either with brood-size or age of nestlings. Males have been found to bring larger food loads in Yellow Warbler (*Dendroica petechia*) at broods of five, but not at broods of three or four (Biermann and Sealy 1982) and in Savannah Sparrows (*Passerculus sandwichensis*) at days 5 and 6 of nestling age, but not earlier or later (Bèdard and Meunier 1983). In the Nashville Warbler, there were no differences between sexes for broods of four or five between the ages of 4 and 8 days.

Males and females within a pair contributed essentially equal amounts of food to nestlings in 9 of 11 pairs observed. Total feeding rates did not differ between the sexes at nine nests, which supports the initial prediction, that in an essentially monomorphic, monogamous passerine with biparental care, each member of the pair should contribute substantially to the rearing of young. Interestingly, at the two nests showing strongly skewed parental contributions, it was the male that contributed very little (only 14% at one nest and nothing at the other). Roth (1977) also reported a complete absence of male help at a Nashville Warbler nest. This lack of male assistance was not related to brood-size (Table 1) or to season (June), or to apparent influence of the blind (the male at nest 11 visited the nest area, within 50 cm of the nest, but not the nest and never with food). The female appeared to compensate for low male help at nest 2; the female's feeding rate at 8.84 was the highest of any individual bird (Table 1), but the rate of feeding of the female at nest 11, where there was no male assistance, was not different from rates of females with equivalent male assistance. Young fledged from both nests, but because their fledging weights were not taken, it is not known if young from nest 11 fledged at a lower weight than young from other nests.

Although a linear relationship between feeding frequency and nestling age has been shown to occur in several passerines (e.g., Howe 1979, Pinkowski 1978), most of the increase actually occurs early in the nesting period (Johnson and Best 1982). In Nashville Warblers, such an increase probably occurs before the nestlings reach 4 days of age; in this study, I show that from 4 days to the day before the young fledge, there is no corresponding increase in feeding rate. The increasing energetic demands of the young are met by the adults bringing in larger prey items as a function of nestling age; there was a significant increase in length of Lepidoptera larvae with increase in nestling age (Fig. 1). Some studies (e.g., Royama 1966, Morehouse and Brewer 1968, Biermann and Sealy 1982) have reported an inverse correlation between feeding rate and size of prey items. In the Nashville Warbler, no such inverse correlation was observed, a finding consistent with that in another paruline, the Prairie Warbler (*Dendroica discolor*) (Nolan 1978).

An increase in feeding rate with increasing brood-size has been found in some passerines (Royama 1966, Morehouse and Brewer 1968, Hussell 1972, Best 1977, Johnson and Best 1982) but not in others (e.g., House Sparrow [*Passer domesticus*], Seel 1969; Eastern Bluebird [*Sialia sialis*], Pinkowski 1978; Savannah Sparrow, Bèdard and Meunier 1983). In the Nashville Warbler, I detected no relation between feeding rate and brood-size in broods of four or five young. Such correlations (or lack thereof) are probably due to a trade-off between food requirements/nestling and

thermoregulatory costs/nestling (i.e., larger broods have a lower heat loss/nestling owing to a lower surface-to-volume ratio).

Although total feeding rates between males and females did not differ significantly, there were significant differences in feeding rates among time periods within a day, and the proportion of diurnal feedings within a sex differed between sexes. Compared to females, males contributed proportionately less in the early morning and in the evening, and more during the late morning and afternoon periods. This difference is possibly a result of different diurnal behavioral patterns of the sexes; during the early morning and evening, males sing, whereas during the mid-day period females brood the young. The lowest brooding time period is between 18:00–21:00 (Roth 1977), which corresponds closely with the highest feeding rate of the female (Fig. 2).

Thus, these results show that both sexes contribute substantially to the feeding of nestlings and that there is no significant difference between males and females in level of contribution (at least, in 9 of 11 nests observed). The nature of the prey did not differ between the sexes, nor did number of prey per feeding trip. Feeding rates were not influenced by brood-size (for broods of four or five) or by age of nestlings (between 4 and 8 days of age), and the increasing energetic demands of the maturing young were met by the adults bringing in larger prey items as the nestlings grew older. Time of day influenced feeding rates, and a proportional difference between the sexes in diurnal feeding rates is probably due to different behavior patterns of males and females within a day.

SUMMARY

Male and female contributions to feeding nestlings were investigated in an essentially monomorphic, monogamous passerine, the Nashville Warbler (*Vermivora ruficapilla*), for two summers in Algonquin Provincial Park, Ontario. The identity, size, and number of prey items per feeding trip did not differ between the sexes. In general, feeding rates were not significantly different between males and females and were not influenced by brood-size between broods of four or five young. Males and females made equal contributions to feeding nestlings, as predicted from mating system theory, at 9 of 11 nests. At the remaining two nests, one male contributed very little (14%), and the other male contributed no food at all.

The number of feeding trips was not influenced by age of nestlings; however, the adults brought in larger prey items as the nestlings grew older to meet the increasing energetic demands of the maturing young. Time of day influenced feeding rates (the highest rates were in the early morning and evening), and the proportion of diurnal feedings within a sex differed between the sexes, probably reflecting a difference in diurnal behavior patterns between males (singing behavior) and females (brooding).

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SYMPATRY IN TWO SPECIES OF MOCKINGBIRDS ON PROVIDENCIALES ISLAND, WEST INDIES

BEVERLEA M. ALDRIDGE

The breeding ranges of two mockingbird species coincide in the West Indies (Fig. 1). The Northern Mockingbird (*Mimus polyglottos*) is found in many parts of the United States and Mexico, the Bahamas, and the Greater Antilles. The Bahama Mockingbird (*M. gundlachii*) occurs in the Bahamas, on cays off the northern coast of Cuba, and in the Hellshire Hills region of south-central Jamaica. *M. polyglottos* is found on nearly all major islands of the southern Bahamas but is usually less common there than *M. gundlachii* (Buden 1979). Conversely, *M. gundlachii* is rare and probably does not often breed in the northernmost Bahamas (sight records only, on Grand Bahama and Abaco).

Although sympatry in avian congeners has been the subject of much study (Grant 1966, Emlen et al. 1975, Hertz 1976), few of these investigations include mimids. During daily observations on Providenciales in the Turks and Caicos Islands, from December 1977–March 1978 and from December 1979–May 1980, I noted ecological and behavioral differences that seem to facilitate sympatry in *M. polyglottos* and *M. gundlachii* in the southern Bahamas.

The two species are easily distinguishable in the field. *M. gundlachii*, the larger, has conspicuous stripes on the back and flanks but lacks the extensive white patches in wing and tail found in *M. polyglottos*. Sexes are similar in both species though *M. gundlachii* females tend to have shorter tails than males. Inter-island and intraspecific variation among these populations have been discussed by Buden (1979).

STUDY AREA AND METHODS

The Turks and Caicos Islands lie on the Turks and Caicos Banks and are the easternmost islands of the Bahamas archipelago (Fig. 1). Although geographically part of the Bahamas, they are a British Crown Colony and are politically separate from the independent Commonwealth of the Bahamas. Providenciales is the northernmost of the six main islands in the Caicos chain. It is a low lying island, 23 km long and 10,500 ha in area.

According to local residents, the rainfall on Providenciales is about 64 cm annually. The heaviest rain begins in April following a dry period. This dry season usually occurs from February to late March and is a time when deciduous trees lose their leaves. The prevailing winds are from the northeast in winter, but southeasterly in summer. On Providenciales the northern coast is comprised of sandy beaches and rocky cliffs. Inland there is arid woodland at lower elevations, and limestone forest on higher ground. Salinas and tidal flats characterize the leeward southern coast where long stretches of beach and rocky terrain border the shallow waters of the Caicos Bank.

FIG. 1. Breeding ranges in the West Indies of *Mimus polyglottos* (shaded areas) and *M. gundlachii* (dashed lines) redrawn from Lack (1976).

Most of the flora is derived from Cuba, Hispaniola, and the United States (Gillis 1974). The vegetation is primarily a dense, low scrubland where poor, thin soil and exposure to salt-laden winds stunt growth; native trees rarely exceed 7 m and most are less than 4 m in height.

The two adjoining study areas which I selected provided ecological contrast and different levels of human interference. Habitat "A" consisted of 7 ha of a hilly ruderal area where a cultivated garden was surrounded by limestone forest. Many solution holes, usually with wild fig (*Ficus citrifolia*) growing in them, were found in the scrub, among trees such as lignum vitae (*Guaiacum sanctum*), sweet acacia (*Acacia farnesiana*), and wild sapodilla (*Manilkara bahamensis*). Habitat "B" consisted of sparse vegetation, a coastal strand and occasional grassy areas. Inland from the beach, low dunes merged into flat arid coastal woodland with sandy soil and many tree branches reaching to the ground. This habitat was bordered by a rock ridge with dense scrub at its base.

I used two methods for counting mockingbirds—a strip census in the first season and direct counting of territorial birds in the second. I used differences in behavior and song to identify the sex of individuals of both species; in most cases these identifications were confirmed during the breeding season. Birds that sang most of the time and showed some aggression toward mates were considered to be males. Birds that were always found perched below singing males were labeled females. In some cases these identifications were confirmed by observations of copulation.

December 1977–March 1978 census.—I censused 7 ha of habitat A by walking a standard route daily at dawn and counting all mockingbirds seen within 18 m on either side. I

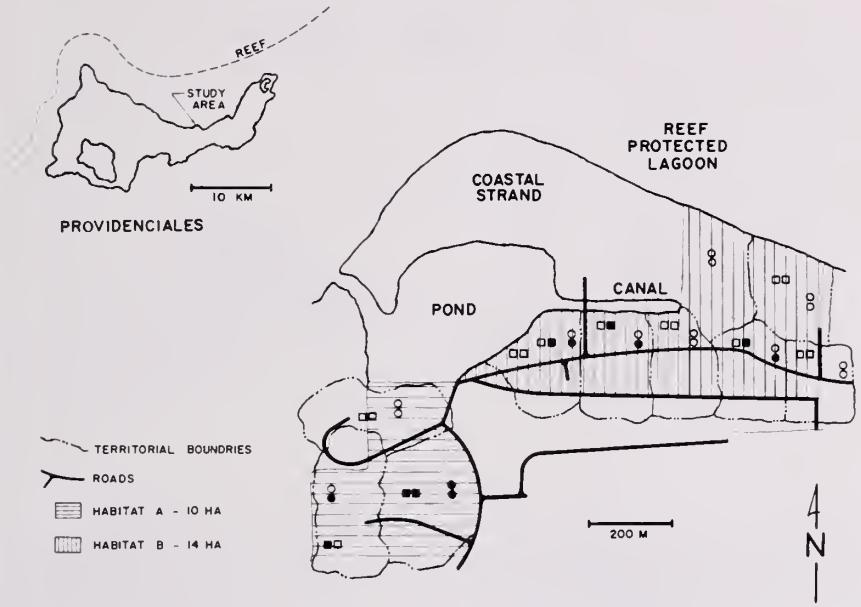

FIG. 2. Study area of Providenciales with territory holding birds and estimated territories. Circles represent *Mimus gundlachii,* and squares represent *M. polyglottos.* White indicates unbanded birds and black indicates banded birds.

occasionally left the route to confirm identification of birds heard but not seen. In December, males of both species were singing throughout the morning hours. Singing *M. gundlachii* males with females perched either beside or below them appeared to be singing to maintain territory. Singing *M. polyglottos* males, without females, appeared to be singing to attract mates and as well as to maintain territory. By late February all mockingbirds in the study areas were paired and apparently singing to maintain territory. Intraspecific border conflicts were common in both species until March when some birds were seen carrying nest material and their behavior indicated that the breeding season had begun.

I attempted to mark with paint or color band as many mockingbirds as possible. By March I had marked six, and two wore colored bands.

December 1979–May 1980 census.—I enlarged the area of habitat A to 10 ha and that of habitat B to 14 ha and attempted to capture and color band all mockingbirds found in both habitats. Birds not captured, but seen repeatedly in the same place, were considered to be territory holders and included in the count. At the same time, differences in behavior and vertical distribution in the vegetation were noted. Periodic surveys were made to count individuals present and determine their breeding status. In a final count on 30 April I found 12 banded and 28 unbanded birds holding territory (Fig. 2). Of these, one pair of *M. gundlachii* and four pairs of *M. polyglottos* were incubating eggs.

To capture birds at the edge of clearings I used a tape recorder and two mist nets strung about 3 m apart. Birds attracted to taped song usually flew over the first net and into the second one. In dense scrub I used the tape recorder with one net. *M. gundlachii* males, in response to taped *M. gundlachii* song descended to the ground to sing with the tape and

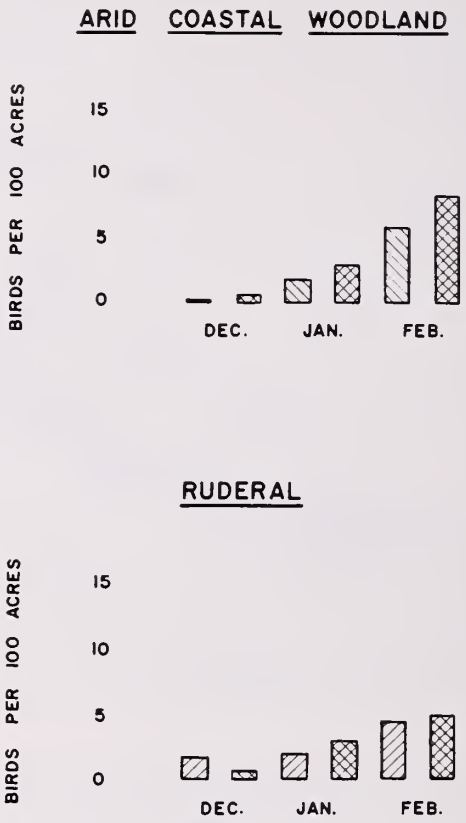

FIG. 3. The mean number of birds observed daily in the arid coastal woodland and ruderal study areas in December, January, and February (diagonal lines = *Mimus polyglottos*, cross-hatching = *M. gundlachii*).

were caught more easily than females. *M. polyglottos* responded to taped song by flying, with females following, toward the net. Members of this species did not descend to the ground and were usually caught near the top of the net.

I estimated territorial boundaries by plotting positions of color-banded birds and noting sites of intraspecific conflict. In some instances a boundary was found for *M. gundlachii* when pairs from adjoining territories approached taped *M. gundlachii* song from opposite directions; only one pair responded in a territorial manner while the other pair watched from a short distance away.

I made tape recordings of songs and calls of both species using an 18¾" (47 cm) parabolic reflector and a Panasonic tape recorder (model R.Q.345) with a tape speed of 1⅞ I.P.S. (5 cm per sec). In addition to using taped sounds to capture birds and determine territory, I performed experiments to assess the response of both species to their own song and to the song of the other species.

TABLE 1

FREQUENCY OF PAIR SIGHTINGS OF *MIMUS POLYGLOTTOS* AND *M. GUNDLACHII* IN ARID COASTAL WOODLAND

Date	Species	No. pairs present	No. birds obs.	Max. possible sightings	%	*Z* value
Dec.	*M. polyglottos*	2	13	6	33%	0.10–0.05
	M. gundlachii	5	13	6	83%	0.10–0.05
Jan.	*M. polyglottos*	14	61	30	46%	0.10–0.05
	M. gundlachii	23	55	27	86%	0.05–0.01
Feb.	*M. polyglottos*	41	114	57	72%	0.05–0.01
	M. gundlachii	58	117	58	100%	0.05–0.01

RESULTS

1977–1978 census.—Fig. 3 shows the population in habitats A and B at the end of each month from December–February. The mean number of birds per day present in A was significantly greater in January than in December (Student's t test, $t = 3.91$, $P \leq 0.01$) and further increased from January to February ($t = 3.33$, $P \leq 0.01$). Similarly in habitat B, the average number of birds per day was higher in January than December ($t = 3.59$, $P \leq 0.01$) and higher again in February than January ($t = 3.23$, $P \leq 0.01$).

Both species were distributed in an approximate 1:1 ratio in both study areas. After pair formation in February one pair of each species shared the 10 ha of habitat A and four pairs of *M. gundlachii* and three pairs of *M. polyglottos* shared the 14 ha of habitat B. Table 1 shows the number of pair sightings given as a percentage of the maximum number possible based on total number of individuals observed. The number of pair sightings was significantly higher for *M. gundlachii* during each of the three census months December–February (Fig. 4).

Habitat preference.—*M. gundlachii* was usually sighted in semi-dense scrub and on high song perches in acacia and sapodilla trees and was seldom seen in open grassy areas where the vegetation was low and very sparse. *M. polyglottos* often shared the semi-dense scrub with *M. gundlachii* as well as many of the high song perches, but was more numerous near human habitation and at the edge of clearings. *M. polyglottos* was most common in sparse scrub and grassland. Both species were found, at least occasionally, in most of the different major habitats on the island including beach strand, scrublands, and arid woodlands.

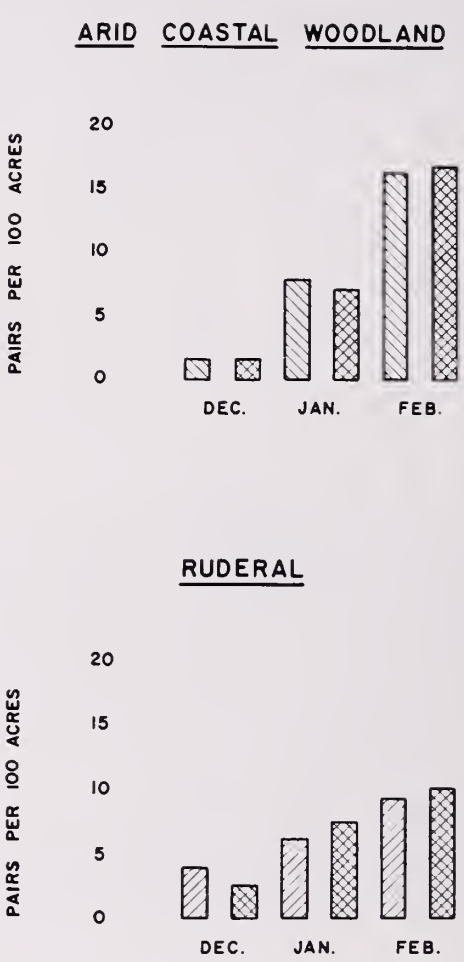

FIG. 4. The mean number of mockingbird pairs observed daily in the arid coastal woodland and ruderal study areas in December, January, and February (diagonal lines = *Mimus polyglottos*, cross-hatching = *M. gundlachii*).

Vertical distribution in vegetation.—Figs. 5 and 6 show daylight observations of the species' vertical segregation and overlap in both habitats. Student's t test for significance of independent means for December–March showed that *M. gundlachii* occupied the highest levels in the vegetation both in habitat A ($t = 1.70$, $P \leq 0.05$) and in habitat B ($t = 4.3$, $P \leq 0.05$).

In habitat A both species frequently shared the same levels after 15

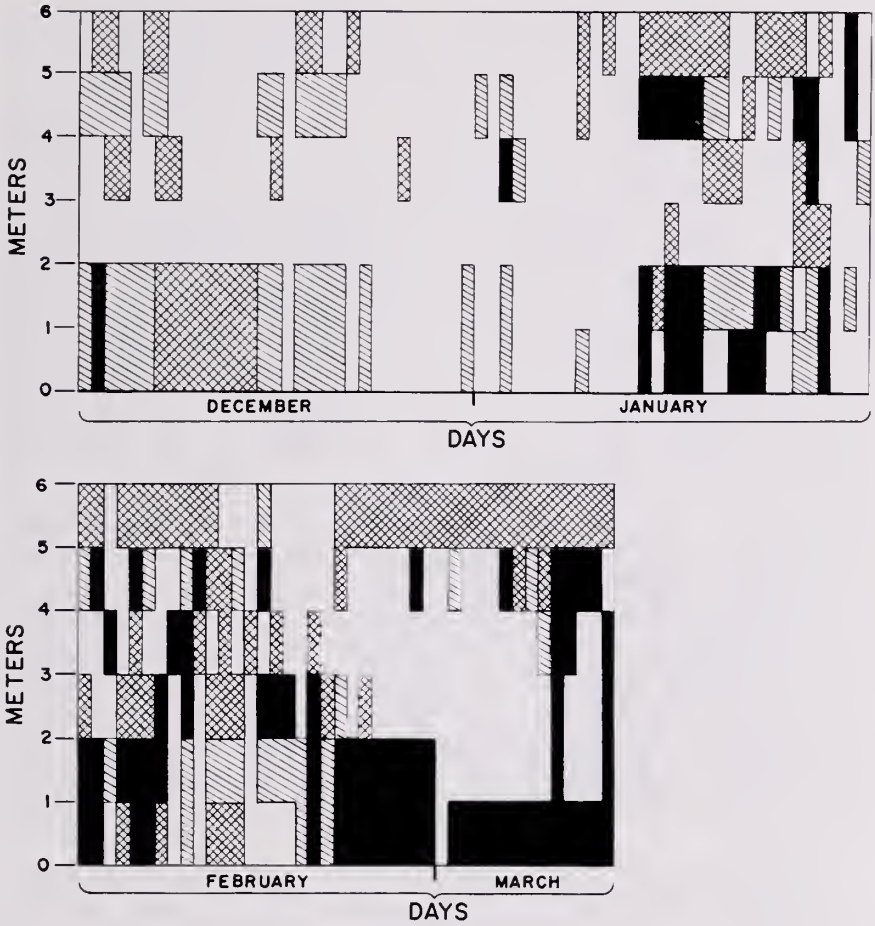

FIG. 5. Vertical distribution of perching birds in the vegetation of the ruderal study area (diagonal lines = *Mimus polyglottos*, cross-hatching = *M. gundlachii*, solid blocks = both species perching together).

January. The presence of both species at ground level can be explained by competition for food, and sharing of high levels during competition for song perches. In habitat B, *M. gundlachii* usually occupied levels above those of *M. polyglottos* (Fig. 6).

Territoriality and food partitioning.—In December interspecific aggression was common between two color-banded pairs of mockingbirds holding territory in habitat A. Aggression was mostly seen between the two males while they foraged at fruit trees or shrubs harboring wooly aphids.

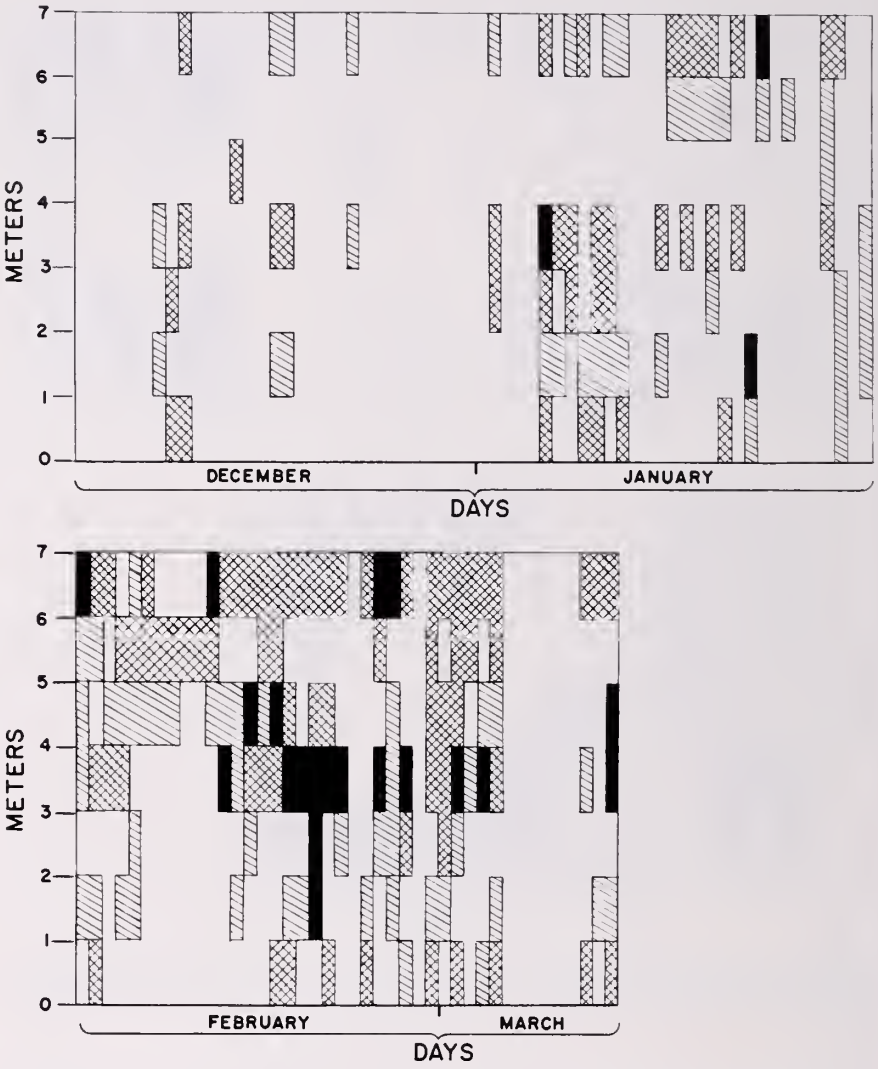

FIG. 6. Vertical distribution of perching birds in the vegetation of the arid coastal woodland study area (diagonal lines = *Mimus polyglottos*, cross-hatching = *M. gundlachii*, solid blocks = both species perching together).

In conflicts over food the male *M. gundlachii* usually put the *M. polyglottos* to flight. Conflicts gradually lessened in early January, each species began foraging at different times and food sharing became apparent. From time to time aggression again occurred at food sources (such as ripening

fruit) as they became available. After initial contact each species began to forage separately and aggression ceased.

The pair of *M. polyglottos* holding territory in habitat disappeared on 4 March. The disappearance could have resulted from recapture; the female was sighted outside the study area but the male was never seen again. This pair had been captured in a trap and seemed to suffer some trauma afterward. Four days later another pair of *M. polyglottos* arrived in the area occupied by the above pair and stayed to forage. Interspecific aggression began again, but in this case the new male *M. polyglottos* attacked the *M. gundlachii* pair frequently. Some encounters ended with abrupt flight by both species, but others involved attacks by *M. polyglottos* on *M. gundlachii*. At times male *M. gundlachii* seemingly remained oblivious, however, on one occasion a male flew directly from his perch landing on the back of a *M. polyglottos* (sex unknown) foraging at a pepper bush (*Capsicum annum*). The attack resembled an attempt at copulation from which the *M. polyglottos* retreated calling vociferously. Aggressive encounters lessened in both numbers and intensity as the *M. polyglottos* pair remained to breed and forage in the same area with the *M. gundlachii* pair.

In habitat B where food was plentiful, only one instance of aggression at a food source was noted. Aggressive displays, however, were common at the song perch of a male *M. gundlachii* marked on wing and tail with orange paint. This male sang longer and more vigorously than others, occupied the highest tree in the habitat, and was often under attack by other *M. gundlachii*. Other singing *M. gundlachii* males were seldom approached by rivals, but in instances when they were the female drove off the intruders.

Between *M. gundlachii* pairs, aggression seemed limited to border conflicts with "growling" and feather-fluffing displays that invariably attracted *M. polyglottos*. In *M. polyglottos* the "attack and chase" intraspecific territorial defense was first noted during mate selection when singing males left the song perch to chase intruders. Growling was common among groups of *M. polyglottos*. Interspecific aggression was observed when five *M. gundlachii*, growling and exhibiting agonistic behavior, were attacked by one *M. polyglottos* in typical "attack and flee" fashion. Interspecific aggression was noted again when one *M. polyglottos* (sex unknown) attacked the orange painted male *M. gundlachii*. In this instance, the *M. polyglottos* adult was accompanied by two juveniles begging for food and it left them to attack the male *M. gundlachii* on his song perch. The *M. gundlachii* retreated and the *M. polyglottos* remained to sing a few phrases before rejoining the young.

Vocalizations.—The primary song of *M. gundlachii* is a series of low

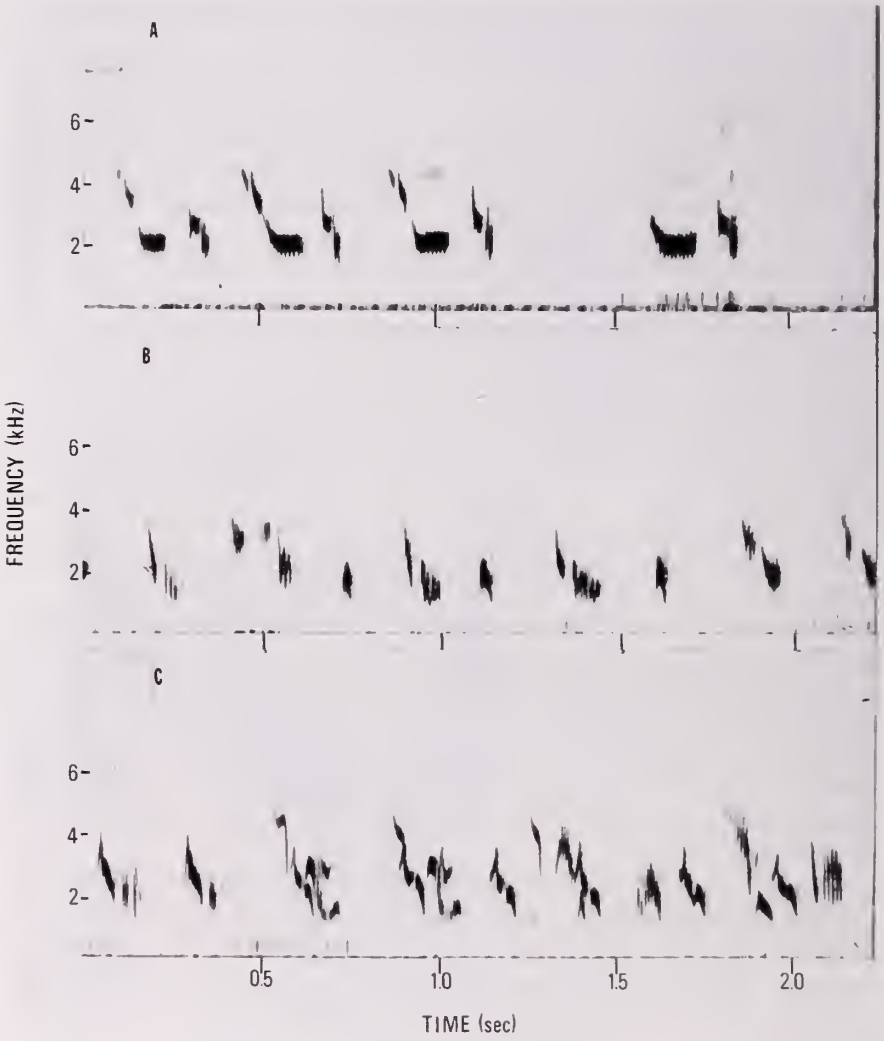

FIG. 7. Songs of mockingbirds from Providenciales Islands: A. *Mimus polyglottus*; B. *M. gundlachii*; C. duet of both species.

reiterated syllables interspersed with occasional trills and chuckles (Figs. 7A and B). It is less strident than *M. polyglottos* whose versatility, defined by the number of song patterns used (Howard 1973), is high. *M. gundlachii* song was heard at different times of the day on almost every day during winter. Individuals of this species were most vocal in March and April when singing began before dawn and continued intermittently until dusk.

M. polyglottos was seldom heard before dawn, but often in the morning. When males began advertising in February, *M. polyglottos* song was heard throughout the daylight hours and sometimes in the evening. Both species sing all winter, but *M. gundlachii* sings more often than *M. polyglottos.*

Growling and chirping were often heard between pairs of both species, but whisper songs were heard only from *M. gundlachii.* Whisper songs are sung from a low perch with closed bill. The alarm call of *M. gundlachii* is a low sharp chirp. In *M. polyglottos* this call is two sharp chirps. To my ear, parts of *M. gundlachii* song seemed similar in pitch, rhythm, and phrasing to that of *M. polyglottos.* The similarities may be the result of mimicking on the part of *M. polyglottos.* On Providenciales I heard *M. polyglottos* mimic the Blackfaced Grassquit (*Tiarus bicolor*), the Blue-gray Gnatcatcher (*Polioptila caerulea*), Ospreys (*Pandion haliaetus*), and American Kestrels (*Falco sparverius*) in the winter months, and Laughing Gulls (*Larus atricilla*) that were courting in April.

Predawn antiphonal singing was common only in *M. gundlachii* and appeared to be a daily ritual unless the weather was stormy. Heard just before dawn, it continued until sunrise. Distinctly different from primary song, it consisted of one or two long phrases repeated note for note by another *M. gundlachii* in an adjoining territory.

Sexual display consisted of short leaps (often accompanied by song) above the song perch. This display was performed by both male and female paired *M. gundlachii,* and male *M. polyglottos.* Individuals of both species used tall trees for song perches; the orange-painted male *M. gundlachii* used the tallest tree in habitat B. The song of this male increased in length and intensity after mid-February. With few pauses, the song lasted 3–4 h. In one instance, a *M. polyglottos* (sex unknown) twice attempted to sing with this male but the female *M. gundlachii* attacked the intruder and it flew away. The female often interrupted this male's song by alighting on the same perch and growling harshly. This behavior was common in *M. gundlachii* females throughout the winter. *M. polyglottos* females exhibited this trait only during the breeding season, and then to a lesser degree.

Specific trees were chosen as song perches and it appeared, like the food sources, they were shared by both mockingbird species. In late February *M. gundlachii* was occasionally seen on a perch usually taken by *M. polyglottos.* Usually, once taken over by *M. gundlachii,* perches were not changed again. In some cases, when a *M. polyglottos* vacated a perch for no known reason, a male *M. gundlachii* would claim it without interspecific aggression. I did see once, however, the use of song for displacement of *M. polyglottos* from a high perch when a male *M. polyglottos,* after advertising from a sapodilla, was challenged by a male *M. gundlachii*

singing below. This male alighted on the song perch and began to duet with the *M. polyglottos* (Fig. 7C). I observed this situation for three successive mornings until the *M. polyglottos* disappeared and the *M. gundlachii* sang alone from the perch every morning. Neither female took part in these incidents but waited quietly in the scrub.

M. gundlachii began singing more vigorously in March. By April, many females were vocalizing with males by interrupting primary song. The song between male and female then became antiphonal. It seemed to represent an intense dialogue between them. Female *M. polyglottos* did not sing at any other time except just before, or immediately after copulation. Sung randomly from a perch, the song is not antiphonal.

Courtship.—Female *M. gundlachii* constantly attended the males. They usually perched below males and when males flew or foraged on the ground, they followed closely behind. Because most *M. gundlachii* were paired by December I was not able to study mate selection in this species. On 2 February I observed what I took to be pre-copulatory behavior in *M. gundlachii* when a female gained attention of the male as he foraged on the ground by approaching and growling. A display followed with the birds circling, bowing and leaping with feathers fluffed and wings drooping. The episode ended when the male, with lowered head, chased the female into the scrub. I did not see any copulations in this species.

When a female *M. polyglottos* responded to male song, acceptance by the male was preceded by male chasing and female avoidance with both birds growling. In one color-banded pair, acceptance took place on 9 December but copulation was not seen until 22 January. In this courtship, mate acceptance, accompanied by excited behavior of both birds, was followed by a quieter period of several weeks of roosting, flying, and foraging together. A change in behavior of a female occurred when she began to appear more often on the song perch with the male, fluffing feathers, growling, and fluttering around him. On one occasion a female called to a singing male from a nearby perch and assumed a crouching posture. The male approached by direct flight and with a slight swoop above the female, settled on her to copulate. This occurred three times during the first day of copulation. The next day the male sang in a subdued manner then suddenly descended to the ground to copulate as the female held nest material in her bill. This behavior was noted twice on the second day, after which I saw no more copulations. This female, and all others observed, uttered loud calls during copulation.

Foraging.—Both species are omnivorous. Food items for both include young anoles (*Anolis* sp.), caterpillars, agave nectar, and a wide variety of seeds and fruits (pers. obs.). While foraging on the ground, both species turn leaf litter and small stones with their bills. Many food items were

too small or were taken too rapidly to identify. *M. gundlachii* ran quickly on sandy soil beneath trees and shrubs searching at random and only stopping to seize and ingest prey. *M. polyglottos* was more deliberate and dug unhurriedly, waiting quietly and often wingflashing. *M. gundlachii* sometimes quivered wings while foraging, but did not usually use the wingflash as a hunting technique. Both species often perched near fruiting trees. Pits were regurgitated, often in the middle of a song.

Response to playbacks.—*M. gundlachii* reacted immediately to playbacks of *M. gundlachii* song and approached to sing antiphonally with the tape. Females, always nearby, sometimes joined their mates in feather-fluffing close to the tape recorder. The pairs circled the recorder and the males often turned, spreading their tail feathers and growling at the females while pecking at them. Although response was weaker with successive playbacks, *M. gundlachii* males never failed to respond. Females, however, did not respond to successive playbacks. Playbacks of female *M. gundlachii* song were ignored by both sexes. When *M. polyglottos* pairs were in breeding condition they responded more readily to playbacks of their own song but never as vigorously as *M. gundlachii*. *M. polyglottos* did not descend to the ground, lost interest faster, was less excited, and more cautious than *M. gundlachii*. *M. polyglottos* females followed males to the tape but kept a short distance away and apart from an occasional growl remained quiet. Neither species responded to the call of the other species, but distress calls of *M. gundlachii* brought *M. polyglottos* to observe.

Wingflashing.—*M. polyglottos* often wingflashed while foraging. Wingflashing commonly occurred on open ground in grassy areas and from low branches before catching an insect. Sudden encounters with *M. gundlachii* and the sight of a baited trap also elicited wingflashes. The wingflash begins as a slow forward motion of the wings with a very slight hesitation before a full stretch above the back. The bird's gaze is fixed on an object, the body is quite still, and the white wing patches are fully exposed. Ten wingflash incidents for different stimuli by a marked *M. polyglottos* in habitat A from 1 December–5 March (when the bird disappeared) were: once, when foraging in a tree; three times, seemingly evoked by the presence of a trap; two times in the presence of *M. gundlachii*; and three times by unknown stimuli. Out of 60 observations there were 19 incidents (31.5%) of wingflashing. Each incident involved anywhere from one–five wingflashes in succession. Wingflashes were uncommon in *M. gundlachii* in which white wing patches were lacking. In this species I saw wingflashing incidents only twice; once on my sudden approach through the scrub and once while this species was foraging on the ground. M. H. Clench (pers. comm.) observed wingflashing in *M. gundlachii* only once—on uninhab-

TABLE 2
NEST MEASUREMENTS FOR *MIMUS POLYGLOTTOS* AND *M. GUNDLACHII*

Species	Date	No. eggs	Outer diam. (cm)	Depth (cm)	Tree species used	Nest height (m)
M. polyglottos	12 Mar. '78	2	20	9	*Casasia clusifolia*	2.0
M. gundlachii	27 Mar. '78	0	23	12	unidentified shrub	1.5
M. polyglottos	22 Jan. '80	1	16	7	*Hypelate trifoliata*	1.5
M. polyglottos	30 Mar. '80	3	16	8	*Hypelate trifoliata*	1.5
M. polyglottos	18 Apr. '80	2	20	9	*Guiaicum sanctum*	2.4
M. polyglottos	19 Apr. '80	3	18	8	unidentified shrub	1.5
M. gundlachii	24 Apr. '80	2	24	12	*Coccothrinax argentata*	1.5

ited Little San Salvador Island (Bahamas). One individual approached to within 60 mm while she was seated on the ground and repeatedly wingflashed at her.

Nidification.—Table 2 provides nesting data for two pairs of *M. gundlachii* and three pairs of *M. polyglottos*. The two nests of *M. gundlachii* were cup-shaped and cryptic and the brownish-gray of the incubating bird blended well with the surrounding vegetation. I saw both sexes bring nest material for construction but was unable to determine whether both birds built the nest. Not all nests were well concealed and those not were probably subject to predation by American Kestrels, Cuban Crows (*Corvus nasicus*), and feral cats (*Felix cattus*). At one nest the male *M. gundlachii* guarded from a tree while the female incubated, but the nest, not well concealed, was left unprotected when both birds flew away together to forage.

M. polyglottos built smaller, cup-shaped nests (made of twigs and bark and lined with palm fiber) than did *M. gundlachii*. One found near human habitation contained bits of rag and tissue. *M. gundlachii* nests were made of similar material (but lacked man-made items in their construction). *M. polyglottos* nests were well concealed and inaccessible when built in the prickly purple shrub (*Oplonia spinosa*) common to the island. Male *M. polyglottos* guard the nest during incubation, help the female find food, and feed the young.

DISCUSSION

Although interbreeding between *M. polyglottos* and *M. gundlachii* has been recorded from New Providence, Bahamas, I saw no evidence of this between the two mimid populations on Providenciales. From this study certain differences in behavior and ecology of the two species have emerged. It seems likely that they are reproductively isolated.

On islands where the total number of birds is limited by area, similar species tend to occupy a wide range of habitats and share common food sources (Crowell 1968). This may be the case with the two mockingbirds on Providenciales but some ecological separation is evident. *M. gundlachii* is not found in grassland and sparsely vegetated regions and is less common near settlements. *M. polyglottos* is found in these habitats as well as in those habitats occupied by *M. gundlachii.*

In examining the function of foraging characteristics, differences, if they are significant, may be species-specific or just local adjustments to the immediate biotic environment (Hamilton 1962). The stationary wingflash foraging of *M. polyglottos* is distinctively different from the haphazard foraging of *M. gundlachii.*

The song of *M. gundlachii* is low pitched and less variable than the intricate, diverse song of *M. polyglottos. M. gundlachii* sings antiphonally with other male *M. gundlachii* and with female *M. gundlachii* during the breeding season. Whisper songs are common in this species but *M. gundlachii* does not mimic other species. During this study *M. polyglottos* did not sing antiphonally or sing whisper songs but did mimic other species.

The behavior of female *M. polyglottos* toward mates differed from that of female *M. gundlachii.* Female *M. gundlachii* frequently interrupted the song of their mates by growling, whereas this behavior was not seen in female *M. polyglottos.*

In response to playbacks of *M. gundlachii* song, female *M. gundlachii* followed their mates to the tape recorder and sometimes fluffed their feathers. Female *M. polyglottos* did not follow their mates to the tape recorder in response to playbacks of *M. polyglottos* song and were less agitated than female *M. gundlachii* in this situation. *M. gundlachii* males responded vigorously to playbacks of their own song: by comparison, *M. polyglottos* males gave a much weaker response to their own song.

When *M. gundlachii* males are singing, *M. gundlachii* females defend the song perch (or the male) against intruders. I did not see *M. polyglottos* females defend the song perch or attack intruders. The male *M. polyglottos* chases intruders away and in defense of territory, attacks.

The inpression gained through my observations on Providenciales is one of *M. polyglottos,* the smaller congener, co-habiting with *M. gundlachii* with apparent compatibility. Interspecific aggression, though present sometimes, does not predominate.

SUMMARY

In the winter months of 1977–78 and 1979–80, I studied the behavior of the Northern (*Mimus polyglottos*) and the Bahama (*M. gundlachii*) mockingbirds on the island of Providenciales in the West Indies. This study was undertaken to help identify the factors that permit sympatry between these congeners.

I conducted censuses in two study areas and collected data on territoriality, song, food requirements, habitat preference, and nidification. Song recordings were made for use in playback experiments and for capture and banding.

Because of differences in habitat choice and use, co-occupancy of habitat by the two species occurs with minimal aggression. Interspecific aggression is rare when food is abundant but common when food is less abundant. Here, after initial aggression, food sites are shared. Interspecific territorial disputes were common and there is evidence that *M. gundlachii* uses song to avoid aggression.

Territorial boundaries were estimated by plotting positions of color-banded individuals. As the breeding season approached, *M. gundlachii* gradually displaced *M. polyglottos* from the highest song perches, often by vigorous song.

Generally the breeding season for both species was the same. However, peaks of breeding in the two species occurred at different times.

ACKNOWLEDGMENTS

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FEMALE-FEMALE PAIRING AND SEX RATIOS IN GULLS: AN HISTORICAL PERSPECTIVE

Michael R. Conover and George L. Hunt, Jr.

The regular occurrence of supernormal clutches (SNCs) in several North American gulls has lead to the discovery of female-female pairings in the Western Gull (*Larus occidentalis*) (Hunt and Hunt 1977), Ring-billed Gull (*L. delawarensis*) (Ryder and Somppi 1979, Conover et al. 1979), Herring Gull (*L. argentatus*) (Fitch 1980, Shugart 1981), and Caspian Tern (*Sterna caspia*) (Conover 1983). While some SNCs may result from polygynous associations (Conover et al. 1979, Lagrenade and Mousseau 1983, Conover 1984a), nest parasitism (Fetterolf and Blokpoel, in press) and egg dumping (Ryder and Somppi 1979), most SNCs have resulted from female-female pairs (Hunt and Hunt 1977, Ryder and Somppi 1979, Conover et al. 1979, Conover 1983, Lagrenade and Mousseau 1983, Conover 1984a). Hence, SNC frequencies are often used as an index of female-female pairing frequencies.

It is unclear why some females pair together rather than with male mates because the reproductive success of these females is often lower than for females paired with males (Hunt and Hunt 1977, Kovacs and Ryder 1983). One hypothesis is that some females pair with the wrong sex due to female masculinization, but this hypothesis has not been supported by the finding that there are no significant hormonal (Wingfield et al. 1982) or behavioral (Hunt et al. 1984) differences between females paired with other females and those paired with males in Western Gulls.

Another hypothesis proposes that female-female pairings occur when some females are unable to obtain male mates (Hunt and Hunt 1977). This hypothesis has been supported by two recent studies. Hunt et al. (1980) found that female Western Gulls outnumbered males in a colony on Santa Barbara Island where female-female pairs are common. Furthermore, Conover and Hunt (1984) tested this hypothesis by experimentally skewing the breeding adult sex ratio at some small Ring-billed and California (*L. californicus*) gull colonies by removing males. They found that SNC frequencies in these colonies were significantly higher than in nearby control colonies.

In this study, we have further evaluated this hypothesis by testing the prediction that females should outnumber males in those gull species and populations where female pairings occur: Ring-billed, California, Herring, and Western gulls. There are historical differences in the occurrence of female-female pairing in these four gull species. In Ring-billed and Cal-

ifornia gulls, SNCs are regularly found in some of the earliest egg collections and literature reports (Conover, 1984b). In Western and Herring gulls, however, SNCs have only been found regularly since 1950 (Hunt and Hunt 1977, Conover 1984b). Consequently, female-female pairings appear to be a new phenomenon in the latter two species but not in the Ring-billed and California gulls. If the male shortage hypothesis is correct, these differences should correspond with sex ratio differences. In this study, we examined the thousands of gull specimens in museum collections to test the following predictions: (1) in Ring-billed and California gulls, adult females should outnumber males regardless of collection date; and (2) in the Herring and Western gulls, females should outnumber males among specimens collected since 1950 but not among those collected before 1940.

METHODS

To assess the sex ratio of gulls, we examined specimens in the U.S. and Canadian museums listed in the acknowledgments. All label data were either personally obtained by us, or in the case of collections which we were unable to visit, by the staff of the institutions in question. For each specimen, we determined its age by plumage (Dwight 1925) and obtained sex of the specimen, collection site, and date from the specimen tag. For each species, we tested whether one sex significantly ($P \leq 0.05\%$) outnumbered the other by using Chi-square tests. Chi-square contingency tables corrected for continuity were used to determine whether the sex ratio differed between specimens collected before 1940 and after 1950.

One problem with attempts to determine the sex ratio of natural populations is the uncertainty that the subjects were collected randomly, thereby reflecting the sex ratio of the population. In most studies on avian sex ratios, the investigators themselves collected the subjects from a population. The drawback of this approach is that one sex may be more vulnerable than the other to the particular collecting technique employed by the investigators or one sex may spend more time at the collection sites than the other, at least during certain hours.

In this study, we took another approach: the examination of museum collections. The advantages of this approach include the very large samples available and the fact that these specimens were collected by hundreds of people at hundreds of locations. Potential problems nonetheless exist with using museum specimens to determine the sex ratio of a population. First, most collectors probably were not concerned with collecting specimens randomly with respect to sex. For gulls, this should not be a serious problem given the similarity in appearance of both sexes; few collectors probably knew or cared which sex they were collecting. Second, one sex may be more likely collected than the other, owing to behavioral differences. Most museum specimens were shot. Burger (1983) showed that this collecting technique favored males over females in Laughing Gulls (*L. atricilla*) and this may also be true for other gull species (P. M. Fetterolf, pers. comm.). If this is true for the species used in this study, our tests for excess females will be conservative. To further evaluate this potential, we also examined museum specimens of most North American gull species (*L. atricilla,* Franklin's Gull, [*L. pipixcan*], Common Black-headed Gull [*L. ridibundus*], Bonaparte's Gull [*L. philadelphia*], Heermann's Gull [*L. heermanni*], Mew Gull [*L. canus*], *L. delawarensis, L. californicus, L. argentatus,* Thayer's Gull [*L. thayeri*], Yellow-footed Gull [*L. livens*], *L. occidentalis,* Glaucous-winged Gull [*L. glaucescens*], Glaucous Gull [*L. hy-*

TABLE 1
SEX RATIOS OF GULL SPECIMENS

Species	All specimens		Adults	
	♂/♀	N	♂/♀	N
California Gull	0.90**	1651	0.97	502
Ring-billed Gull	0.77**	2053	0.81*	569
All North American gulls	0.94	17,083	1.07**	6137

* $P \leq 0.05$ (different from 1 to 1 ratio).
** $P \leq 0.01$ (different from 1 to 1 ratio).

perboreus], Great Black-backed Gull [*L. marinus*], and Black-legged Kittiwake [*Rissa tridactyla*]) to determine the sex ratio for museum gull specimens in general.

RESULTS

In both Ring-billed and California gulls, specimens of females significantly outnumbered those of males when all age classes of each sex were pooled. In both species, adult females outnumbered males, but only in Ring-billed Gulls were there significantly more adult females than adult males (Table 1). Thus, the Ring-billed Gull data support the male shortage hypothesis, but the California Gull data do not. In contrast, males significantly outnumbered females among adult specimens when data from all North American gull species were combined. This finding reduces the likelihood that female Ring-billed and California gulls were preferentially collected or were more vulnerable than males to the employed collecting techniques.

When all age classes were combined, Ring-billed and California gull specimens had similar sex ratios before 1940 and after 1950 (Table 2). This result was predicted because there has been no change in SNC frequencies in these two species since 1950 (Conover 1984b). Too few adult Ring-billed and California gull specimens have been collected since 1950 to allow a comparison with the sex ratios of adults collected before 1940.

Among Western Gulls, the male/female ratio was lower among post-1950 than pre-1940 specimens. This difference was statistically significant for both adults alone and for all age classes combined (Table 2). In Herring Gulls, the male/female ratio for both adults and all age classes combined was also lower among specimens collected since 1950, but the differences were not statistically significant due to the small number of specimens collected since that date. These results support the prediction of a post-1940 shift in sex ratios in Western Gulls but not in Herring Gulls. Among

TABLE 2
SEX RATIOS OF GULLS COLLECTED BEFORE 1940 OR AFTER 1950

	All specimens				Adults			
	pre-1940		post-1950		pre-1940		post-1950	
Species	♂/♀	N	♂/♀	N	♂/♀	N	♂/♀	N
California Gull	0.90	1551	0.96	100	—	—	—	—
Ring-billed Gull	0.76	1971	1.05	82	—	—	—	—
Western Gull	1.04	1365	0.55**	186	1.16	471	0.43**	66
Herring Gull	0.88	2186	0.68	114	1.03	780	0.42	27
All North American gulls	0.96	14,428	0.75**	988	1.08	4273	0.82**	266

** $P \leq 0.01$, pre-1940 vs post-1950.

all North American gull species combined, the adult male/female ratio has dropped significantly from 1.08 for pre-1940 specimens to 0.82 for post-1950 specimens.

DISCUSSION

In our examination of museum specimens of gulls, we found significant intraspecific shifts in sex ratios between birds collected before 1940 and after 1950 for all North American gull species combined and for Western Gulls. Before 1940, male Western Gulls appear to have outnumbered females, but among specimens collected since 1950 females outnumber males by over 2 to 1. This significant decrease in the male/female ratio occurred at or before the recent appearance of SNCs and female-female pairs in this species.

A recent change in sex ratio may not be unique to Western Gulls. In Herring Gulls, the adult male/female ratio has dropped from 1.0 for specimens collected before 1940 to 0.5 for birds collected since 1950, although the difference is not statistically significant due to the small number of Herring Gulls collected since then. Female-female pairings may also be a recent phenomenon in this species (Conover 1984b). In contrast, there is, if anything, a slight increase in the male/female ratios of Ring-billed and California gulls from pre-1940 to post-1950, as predicted for species with a long history of SNCs.

While these estimates of sex ratio probably do not represent precisely the sex ratio in the various gull populations, the changes or lack of changes within species over time should be valid indices of the change or lack of change in the sex ratios of the populations sampled. Distortions of sex ratios due to species-specific behavior or collecting techniques are likely and are of major concern when investigators attempt to determine ab-

solute values for sex ratios or to compare sex ratios between distantly related taxa. In the present case, our comparisons are within a species over time, or between closely related species. For these very limited comparisons, there is little likelihood that the potential bias would strongly affect our results. It is unreasonable to assume that changes in either species-specific behavior or collecting techniques would cause increases in the male/female ratio for some species and decreases in others.

This study leaves unanswered the question of whether sex ratios of museum specimens accurately reflect the absolute sex ratio of gull populations. The sex ratios obtained in this study, however, are similar to those obtained by other means. Johnston (1956) found an adult male/female ratio of 0.83 for California Gulls in California. Behle (1958) sexed California Gulls at a Utah colony and found a 1.06 male/female ratio. Our study revealed a ratio of 0.97 for adult California Gull specimens, a value which falls between these two values and is not statistically different from either of them. Hunt et al. (1980) captured 606 adult Western Gulls on Santa Barbara Island in 1977 and 1978 and found a 0.26 male/female ratio. However, based on the proportion of female-female pairs in the colony, they calculated a sex ratio of 0.67. In our study, we found for post-1950 Western Gull specimens an adult sex ratio of 0.43, a value intermediate between their two reported estimates. These authors further reported that for 2–3 year old Western Gulls, the male/female ratio was 0.67, close to our value of 0.60 for immature Western Gull specimens obtained since 1950. Hence, both our results and those of Hunt et al. (1980) have shown that females significantly outnumber males in Western Gulls.

Why should there be a shortage of breeding males in some gulls? Fry and Toone (1981) hypothesized that a shortage of breeding males in Western Gulls was caused by DDT pollution. They argue that sublethal doses of DDT feminize male embryos, causing mature males to forego breeding. This would alter the adult sex ratio at breeding colonies, but not the adult sex ratio of the population as a whole. Our results suggest an alternate hypothesis. Hunt et al. (1980) found a 0.67 male/female ratio among breeding adults at one colony. This is higher than the 0.43 male/female ratio we found for adults collected since 1950. Few of the specimens in the museum collections were obtained from breeding colonies, so our value should reflect the general adult sex ratio. Thus, our data suggest that the shortage of males at the breeding colonies results from a low male/female ratio in the adult population as a whole and not from the failure of feminized males to breed. Therefore, we suggest that the recent occurrence of female-female pairings and the skewed sex ratio in Western Gulls stems from high differential male mortality.

SUMMARY

We evaluated the hypothesis that female-female pairings result from a shortage of breeding males by using museum specimens to test the hypothesis' following predictions: (1) females should outnumber males regardless of collection date in Ring-billed and California gulls, two species where supernormal clutches and presumably female-female pairings have occurred for many years; and (2) in Herring (*Larus argentatus*) and Western (*L. occidentalis*) gulls, the male/female ratio should have decreased since 1950, given the occurrence of female pairings only since then in these two species. The results showed that some, but not all, of these predictions were accurate. Based on museum collections, adult females significantly outnumbered males in Ring-billed Gulls (*L. delawarensis*) but not in California Gulls (*L. californicus*). In both Western and Herring gulls, the male/female ratio was lower among adults collected since 1950 than among those collected earlier, but the differences were not statistically significant in the latter species due to the small number of Herring Gulls collected since 1950.

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COMPARISONS OF ASPECTS OF BREEDING BLUE-WINGED AND CINNAMON TEAL IN EASTERN WASHINGTON

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Blue-winged (*Anas discors*) and Cinnamon (*A. cyanoptera*) teal are closely related members of the blue-winged duck group (Johnsgard 1965, McKinney 1970). Habitat selection, social behaviors, and plumages of females and juveniles of these teal species are quite similar (Johnsgard 1965, McKinney 1970, Bellrose 1976, Palmer 1976). The species' ranges overlap in many parts of the Northwest, although the Blue-winged Teal is a relatively recent pioneer in eastern Washington (Wheeler 1965, Connelly 1978). Strong similarities in ecological requirements and behavior indicate that niches of the two species must overlap, but coexistence over major portions of their breeding and wintering range suggests that differences probably exist. The purpose of this study was to examine the hypotheses that breeding time budgets, habitat selection, and social behavior were the same in the two species.

STUDY AREA AND METHODS

The study was conducted on the Columbia National Wildlife Refuge, approximately 13 km northwest of Othello in Grant and Adams counties of central Washington. The refuge encompasses 11,600 ha, mainly within a portion of the Channeled Scablands known as the Drumheller Tract (Johnsgard 1955, Bretz 1959). Since the early 1950s, wetlands in the area have increased in number, size, and permanence as a direct result of the Columbia Basin Irrigation Project. The ratio between Cinnamon and Blue-winged teal numbers on the study area has varied markedly over the past three decades, and was approximately 3:1 at the time of this study. In combination, the two species comprised about 60% of the breeding waterfowl population in the area (Ball et al. 1977, Connelly 1978).

From mid-April through mid-June of 1975 and 1976, pairs and lone males that were thought to be paired were observed; males were considered paired if they showed aggressive behavior typical of territorial defense (Stewart and Titman 1980). Observations were conducted on four study ponds, each less than 1 ha in area and containing less than 50% emergent vegetation. Each of the ponds was used by one to at least three pairs of each teal species. Habitat in the ponds was grossly classified as mudflat, open water, or emergent vegetation. Floating, unrooted, live plants, and floating debris were included in the emergent vegetation category. The activity and habitat occupied by each member of a pair were recorded at 1-min intervals that were established using a modified metronome timing device (Wiens et al. 1970). All social interactions were recorded whenever they were observed. On the few occasions when birds were screened from view, activities were recorded as unknown. Observation effort was apportioned into three time periods (05:00–10:00, 10:01–15:00, and 15:01–20:00 h) at a ratio of approximately 40:30:30. Whenever possible we changed the species being observed each hour to allow equal sampling of both species throughout the

TABLE 1

TIME BUDGET ANALYSIS OF BLUE-WINGED AND CINNAMON TEAL ACTIVITIES IN THE BREEDING SEASON

	N[a]	Percent of time spent					
		Feeding	Resting	Locomotion	Comfort movement	Alert	Social interactions
Blue-winged Teal							
Females	982	66.9	14.4	10.1	5.4	2.5	0.7
Males	1012	61.9	5.7	15.3	5.4	5.8	5.8
Combined	1994	64.3	10.0	12.7	5.4	4.2	3.3
Cinnamon Teal							
Females	1370	63.1	12.8	11.8	6.1	5.0	1.3
Males	1413	50.5	12.5	14.2	6.8	11.8	4.2
Combined	2783	56.7	12.6	13.0	6.5	8.4	2.7

[a] N/60 = bird h of observation.

breeding season. Differences in time budgets and habitat use were examined using Chi-square tests.

Many methods have been proposed for describing niche overlap (Horn 1966, Hurlbert 1978), but we chose Schoener's (1968) method because of arguments presented by Abrams (1980) and Linton et al. (1981). Overlap was estimated using the formula $N_o = 1 - \frac{1}{2} \sum_{i=1}^{n} |p_i - q_i|$, where N_o represents niche overlap, p_i is the frequency of habitat or feeding method used by Blue-winged Teal, and q_i is the frequency of habitat or feeding method used by Cinnamon Teal.

RESULTS

Time budgets were generally similar between the two species (Table 1). Although males and females of both species spent the majority of their time feeding, males spent significantly less time feeding than females (Blue-winged Teal: $\chi^2 = 5.47$, df = 1, $P < 0.025$; Cinnamon Teal: $\chi^2 = 46.47$, df = 1, $P < 0.001$). Proportion of time spent feeding was significantly lower in male Cinnamon Teal than in male Blue-winged Teal ($\chi^2 = 30.59$, df = 1, $P < 0.001$), but females did not differ significantly ($\chi^2 = 1.31$, df = 1, $P > 0.05$) in this respect. Females of both species also consistently spent relatively more time than males in resting, and less time in locomotion, alert postures, and social interactions.

Habitat use and feeding methods were virtually identical between the sexes (Connelly 1977), and female ducks are thought to play a dominant role in selection of feeding sites (G. A. Swanson, pers. comm.); consequently, we chose to present only data from females in our analyses of feeding habitat use and methods.

TABLE 2

PERCENTAGE USE OF HABITAT TYPES BY FEEDING BLUE-WINGED (BWT) AND CINNAMON TEAL (CT) FEMALES IN FOUR STUDY PONDS

	Pond							
	1		2		3		4	
Habitat	BWT	CT	BWT	CT	BWT	CT	BWT	CT
Open water	62	49	96	54	30	17	7	3
Emergents	22	33	4	41	62	80	93	94
Mudflats	16	18	0	5	8	3	0	3
N[a]	552	747	377	389	135	186	209	412
Overlap[b]	0.87		0.58		0.83		0.96	

[a] Number of feeding observations; N/60 = bird h observed feeding.
[b] Schoener (1968).

Feeding Cinnamon Teal used emergent vegetation more than expected (based on proportional availability of habitats) on all study ponds (χ^2 values = 30.67–352.56, df = 2, P's < 0.001). Blue-winged Teal did likewise on three of the four ponds (χ^2 values = 9.80–155.03, df = 2, P's < 0.01). We did not statistically compare feeding habitat use between the two species, but within each wetland Blue-winged Teal were more likely than Cinnamon Teal to feed in open water habitats (Table 2). The reverse situation held in emergent vegetation, but no consistent difference was detected on mudflats. Overlap values for feeding habitat varied from 0.58–0.96 ($\bar{x}$ = 0.81, SD = ±0.16), where a value of 1.0 indicates complete overlap (Schoener 1968).

Dabbling was the feeding method most commonly used by both species overall, but methods differed greatly among habitat types and study ponds. In fact, we found no difference in feeding methods between Blue-winged and Cinnamon teal that was consistent across the four study ponds, even when habitat types were considered separately (Table 3). Overlap values for feeding methods ranged from 0.30–0.98 ($\bar{x}$ = 0.68, SD = ±0.29) in open water and from 0.40–0.97 ($\bar{x}$ = 0.72, SD = ±0.25) in emergent vegetation.

We observed 121 interspecific social interactions; 86 (71%) of these interactions were initiated by Blue-winged Teal and only 35 (29%) by Cinnamon Teal, in spite of the fact that Cinnamon Teal outnumbered Blue-winged Teal by about three to one. Where the outcome of the interaction could be determined, the bird initiating the encounter was the victor in over 90% of all cases (Connelly 1977). Thus, Blue-winged Teal appear to be more aggressive in interspecific social interactions than are Cinnamon Teal. Further support for this contention is offered by the fact

TABLE 3

FREQUENCY (%) OF FEEDING METHODS USED BY FEMALE BLUE-WINGED (BWT) AND CINNAMON TEAL (CT) IN DIFFERENT PONDS AND HABITATS

Habitat	Feeding method	Pond 1 BWT	Pond 1 CT	Pond 2 BWT	Pond 2 CT	Pond 3 BWT	Pond 3 CT	Pond 4 BWT	Pond 4 CT	Combined BWT	Combined CT
Open water	Dabbling[a]	49	20	35	36	5	10	100	30	41	25
	Tipping up[b]	6	14	0	0	3	0	0	52	3	10
	Hawking[c]	9	1	65	63	5	19	0	0	36	23
	Head under[d]	36	65	0	1	87	71	0	8	21	42
	N[e]	344	367	362	211	39	31	15	13	760	622
	Overlap[f]	0.63		0.98		0.81		0.30			
Emergent	Dabbling	83	55	80	66	59	74	96	95	84	76
	Tipping up	0	4	0	3	0	0	2	0	1	2
	Hawking	4	2	20	1	0	0	0	0	1	1
	Head under	13	39	0	30	41	26	2	5	14	21
	N	111	238	10	159	85	147	194	388	400	932
	Overlap	0.40		0.67		0.85		0.97			
Mudflats	Dabbling	100	99	0	100	100	100	0	100	100	99
	Hawking	0	1	0	0	0	0	0	0	0	1
	N	88	131	0	17	11	5	0	11	99	164

[a] Dabbling—prolonged immersion of some or all of bill; eye is not immersed.
[b] Tipping up—head and neck are immersed and tail is elevated above the water surface.
[c] Hawking—disjunct pecking movements at individual food items on the water surface.
[d] Head under—head is immersed past the eye but tail remains at the water surface.
[e] N/60 = bird h of observed feeding.
[f] Schoener (1968).

that Blue-winged Teal used active hostile displays in 56% of all interspecific interactions vs 22% of active displays by Cinnamon Teal (Table 4). Similarly, in intraspecific hostile interactions, Blue-winged Teal used active displays in 50% of their encounters and Cinnamon Teal used active displays in only 28% of their encounters.

DISCUSSION

Time budgets and aggressiveness of breeding ducks may vary substantially through the stages of the breeding cycle, and spurious distinctions might be inferred if two species were observed at different stages. However, the breeding chronology of Blue-winged and Cinnamon teal appears similar (Yocom and Hansen 1960, Dwyer 1976, Connelly 1977), and we believe that comparisons between the two species are justified. The general pattern of relatively high foraging rates and few occurrences of alert postures and social interactions in female Blue-winged and Cinnamon teal

TABLE 4
COMPARISON OF DISPLAYS USED BY BLUE-WINGED (BWT) AND CINNAMON TEAL (CT) IN SOCIAL INTERACTIONS

	Interspecific		Intraspecific	
	BWT %	CT %	BTW %	CT %
Passive displays[a]				
Hostile pumping	34	67	47	66
Threat	7	11	3	2
Inciting	3	0	0	4
Subtotal (N)	44 (18)	78 (14)	50 (19)	72 (40)
Active displays[b]				
Chase	46	22	39	26
Rush	10	0	8	0
3-bird flight	0	0	3	2
Subtotal (N)	56 (23)	22 (4)	50 (19)	28 (16)
Total (N)	100 (41)	100 (18)	100 (38)	100 (56)

[a] Passive displays involve little or no movement toward another bird.
[b] Active displays involve pursuit of another bird.

was similar to the situation seen in Blue-winged Teal, Northern Shovelers (*Anas clypeata*), and Gadwalls (*A. strepera*) (Dwyer 1975, Afton 1979, Stewart and Titman 1980). Female teal in our study spent 63.1–66.9% of their off-nest time in feeding, bracketing the 65.5% figure presented for prenesting-incubating Blue-winged Teal females in Manitoba (Stewart and Titman 1980). Male Blue-winged Teal in our study spent nearly twice as much time feeding as did the Manitoba males, suggesting that we may have observed some postbreeding males. Relatively low foraging rates by male Cinnamon Teal in comparison to male Blue-winged Teal may imply differences in foraging efficiency, but also may be related to the fact that male Cinnamon Teal spent nearly twice as much time as male Blue-winged Teal in alert postures. Most alert postures appeared related to actual or potential social encounters.

Johnsgard (1955) studied breeding waterfowl near our study area and suggested that Cinnamon Teal tended to use wetlands with more emergent vegetation than those used by Blue-winged Teal, although he cautioned that his sample size was small. Clearly, habitat use overlaps a great deal between the two species and also varies among wetland types, presumably in response to differing distribution of resources. Still, our data support the idea that Cinnamon Teal are more likely than Blue-winged Teal to feed in emergent vegetation.

Ecological significance of the niche overlap value for feeding methods

is difficult to assess. Our approach, lacking individually identifiable birds, prevented the estimation of intraspecific variation in feeding methods. That variation could provide a baseline for comparison to interspecific variation.

The relatively recent pioneering of Blue-winged Teal into historic Cinnamon Teal range (Wheeler 1965, Connelly 1978) has created a situation where intensive competition would be expected. Habitat use and feeding methods can be almost identical between the species, at least on some wetlands. Territorial defense in the blue-winged ducks may be advantageous in providing the female with undisturbed access to food resources that are critical to the breeding effort (McKinney 1973, 1975; Seymour 1974; Afton 1979; Stewart and Titman 1980). We believe that male Blue-winged Teal, because of their aggressiveness in social interactions, probably have a competitive advantage over Cinnamon Teal in maintaining access to preferred areas, thus helping Blue-winged Teal to become established in an area populated by Cinnamon Teal. Hybridization (Connelly 1977, Bolen 1979, Lokemoen and Sharp 1981) and efficiency of resource use will also affect the eventual outcome of the interaction between the two species; these aspects of the relationship remain virtually unknown.

Statistical comparisons of time budget and habitat use data presented in this paper must be interpreted cautiously. Because we did not mark birds, the total number of individuals studied is unknown; hence the presence of one or more atypical birds in our sample could cause serious, undetected bias in the results. Consequently, we have taken what we feel is a conservative approach in analysis. Furthermore, we urge that the results be tested in other areas, hopefully with marked pairs.

SUMMARY

Time budgets, habitat use, feeding methods, and social behavior of breeding Blue-winged (*Anas discors*) and Cinnamon (*A. cyanoptera*) teal were studied during the breeding seasons of 1975 and 1976 in eastern Washington. Time budgets were similar between the two species. Females fed and rested relatively more than males and spent less time in locomotion, alert postures, and social interactions. Blue-winged Teal were slightly, but consistently, more likely than Cinnamon Teal to feed in open water. Feeding methods overlapped substantially between the two species and varied greatly among habitat types and study ponds. Male Blue-winged Teal were more aggressive than male Cinnamon Teal in both intra- and interspecific social interactions.

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WILDLIFE BIOLOGY, DEPT. ZOOLOGY, WASHINGTON STATE UNIV., PULLMAN, WASHINGTON 99164. (PRESENT ADDRESS: IDAHO DEPT. FISH AND GAME, BOX 1336, SALMON, IDAHO 83467 (JWC); MONTANA COOPERATIVE WILDLIFE RESEARCH UNIT, UNIV. MONTANA, MISSOULA, MONTANA 59812 (IJB). ACCEPTED 21 JUNE 1984.

JOINT MEETING OF COOPER ORNITHOLOGICAL SOCIETY AND WILSON ORNITHOLOGICAL SOCIETY

The fourth joint meeting of these societies will be held 5–9 June 1985, at the University of Colorado, Boulder. A 3-day scientific program is scheduled involving contributed papers and several half-day mini-symposia. Early morning field trips are planned to ponderosa pine forests in the foothills, water bird habitats and heronries on the prairie, and open meadows, coniferous and aspen forests in the mountains. All day field trips on 9 June will tour Rocky Mountain National Park or Pawnee National Grassland. Spouse-guest tours will go to historical and art museums in Denver, the Air Force Academy and Broadmoor Hotel in Colorado Springs, the Coors Brewery, and Central City, an historical gold-rush town. The banquet will be held at the Denver Museum of Natural History. The Wilson Society is sponsoring the Sutton competition for excellence in painting of birds by amateurs. The meeting announcement will be mailed in January and abstracts are due by 6 March 1985. Questions can be directed to Dr. Cynthia Carey (local committee on arrangements) or Dr. Carl Bock (scientific program) at: Department of EPO Biology, University of Colorado, Boulder, CO 80309.

Wilson Bull., 96(4), 1984, pp. 634–646

THE KALIJ PHEASANT, A NEWLY ESTABLISHED GAME BIRD ON THE ISLAND OF HAWAII

VICTOR LEWIN AND GERALDINE LEWIN

Kalij Pheasants (*Lophura leucomelana* ssp.) comprise a complex of nine subspecies within the gallopheasant group whose distribution extends from the Indus River of Pakistan in the western Himalayas, eastward through northern India, Nepal, Sikkim, Bhutan, and south through Burma to western Thailand (Delacour 1949). They are sedentary in forested foothills and mountainous country from 600–3400 m elev. along woodland roads, brushy ravines, and at the edges of forest clearings, but may move to lower elevations during winter (Bump and Bohl 1961, Bohl 1971).

Kalij Pheasants are easily raised in captivity and were present in European avicultural collections as early as 1857 (Gerrits 1974). They subsequently became common in American game farms, and following the turn of the century were first liberated into North American forests by the Connecticut Game Commission. Between 1962 and 1976 they were released in Tennessee, Virginia, Oregon, Washington, and British Columbia (Bohl and Bump 1970, Bohl 1971, Banks 1981). Apparently no sustained breeding populations resulted from these releases. In 1962 Kalij Pheasants were one of the many species of exotic game birds released at Puu Waawaa Ranch on the Island of Hawaii as part of the extensive liberation program conducted by the owners of the ranch (Lewin 1971). The present population on the Island of Hawaii is believed to have been derived solely from this release which consisted of 67 birds taken from Michigan and Texas game farms. Following release, Kalij Pheasants became so widespread and abundant that they were declared a legal game species in 1977.

Kalij live in close proximity to several endangered endemic forest birds (van Riper 1973, Sakai and Ralph 1978, van Riper and Scott 1979) on Hawaii island and are being considered for release at other locations within the State. However, nothing is known of their basic biology and the possible impact they might have on native fauna or flora via their food preferences, as reservoirs of disease (especially malaria), or indirectly by seed dissemination of exotic plant pests. It was for these reasons that we undertook to describe the successful colonization, food habits, behavior, and reproductive phenology of Kalij Pheasants on Hawaii island.

METHODS

Kalij Pheasants were studied from 29 January–25 June 1981. Forty-four pheasants were collected from widely separated areas on Hawaii island; however, most were from the Kona

Coast (36 were taken from the Makaula Ooma Forest Reserve, 5 from the Honaunau Forest, 1 from Manuka Forest Reserve, 2 from the Hamakua Coast, and 1 each from Humuula and Laupahoehoe forest reserves).

All pheasants were necropsied between 1–4 h after collection. Parasites were collected by standard techniques and results are reported separately (Lewin and Mahrt 1983). Standard body measurements were recorded, ovaries preserved in 10% formalin and the condition of the pre- and postovulatory follicles determined later under a dissecting microscope. Testes were preserved in Bouin's Solution, sectioned at 7 μ, stained with Heidenhain's Haematoxylin and counterstained with Eosin Y. Dating of ovarian events and determination of stages of spermatogenesis follows Lewin (1963). Contents of the crop and gizzard were preserved in 10% formalin.

Study skins were prepared from 10 pheasants for taxonomic determination. Eight have been deposited in the University of Alberta Museum of Zoology and two are in the Bernice P. Bishop Museum, Honolulu. The history of colonization and present distributional pattern are based on our observations supplemented by information from local biologists, ranchers, and land managers, and from previously published records (Pratt 1976, Katahira 1978, Mull 1978, Paton 1981). Scientific names of plants follows St. John (1973) while common Hawaiian plant names are from Porter (1972).

RESULTS

Taxonomy.—The nomenclature of Delacour (1949) was followed for the subspecies of *Lophura leucomelana.* Identification proved to be difficult as most of six males and four females prepared as study skins appeared to represent intergrades between the White-crested Kalij (*L. l. hamiltoni*) and the Nepal Kalij (*L. l. leucomelana*). These represent the westernmost of the nine subspecies described from their native Asian range. In the Western Himalayas the White-crested Kalij occurs from 366–3353 m elev. and in Nepal the black crested Nepal Kalij occurs from 1219–3048 m.

Dispersal.—The present population of Kalij Pheasants on Hawaii island results from a single release in 1962 at Puu Waawaa Ranch Headquarters of 67 birds. Shortly after their release they established a small breeding population in the exotic silk oak (*Grevillea robusta*) forest immediately above the release site. They were confined to this small plantation for the following 5 years.

Their subsequent dispersal across the island was reconstructed from 360 sight records collected since pheasants began their movements from Puu Waawaa (Fig. 1). Dispersal was in four directions, and by 1966 they had moved southward around both sides of Mt. Hualalai. By 1971 they were established on the upper Kona Coast above Kailua, after which they spread rapidly southward through the mid-elevation forests. By 1979 a few had dispersed around the southern flank of Mauna Loa and were seen only rarely at the southeastern margin of the Kau Forest. At present they are apparently absent from the central Kau Forest.

The eastern half of the island was populated by Kalij Pheasants which

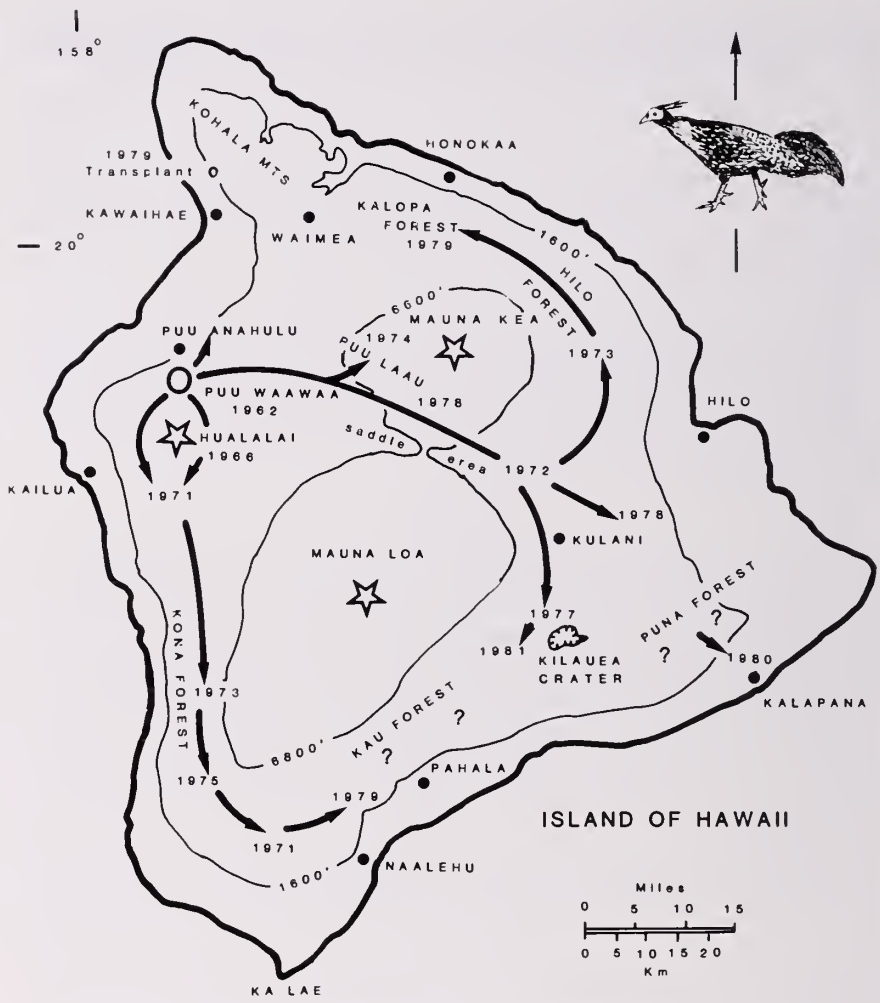

FIG. 1. Routes and dates of Kalij Pheasant dispersal on the Island of Hawaii from their original release site at Puu Waawaa.

moved from Puu Waawaa eastward through the drier saddle region (Fig. 1). By 1972 they had reached the mesic Hilo Forest which contained their preferred dense forest habitat. They subsequently moved southwest to the eastern edge of the Kau Forest (1981); southeast to the Kulani area (1978); and then rounded the eastern flank of Mauna Kea (1973). They reached their northernmost extension in 1979 at Kalopa Forest on the upper Hamakua Coast, where they are now common. The three extralimital

records of Kalij at Ka Lae, Kalapana (Paton 1981) and Hilo were of single adults near sea level, all at least 24 km from the main part of the inhabited range.

Kalij Pheasants dispersed at a rate of approximately 8 km/year and in 14 years colonized a major portion of mid-elevation forests on Hawaii island. Kalij have not yet colonized the central Kau or Puna forests, although this habitat appears suitable, nor have they penetrated farther north on the Kona Coast than Puu Anahulu, presumably because of the dry grassland barrier beyond. Their absence in the Kohala Mountains is apparently due to extensive grassland and sugar cane plantation barriers north of the Kalopa Forest population. However, in 1979, six Kalij Pheasants were transplanted to Konokoa Gulch north of Kawaihae on the west, lower flank of Kohala Mountain. The release site was in dense forest with permanent water. The upper extension of this gulch terminates in grassy pasture, however, and does not afford continuous forest cover with the central and densely forested Kohala range. Kalij, nevertheless, may eventually reach and colonize this extensive forest tract as they are capable of dispersal through marginally suitable terrain.

Analysis of occurrence records by elevation revealed that, although Kalij have been observed from sea level to 2450 m elev., 95% of the sightings were between 450 and 2150 m (Fig. 2). Utilizing the known distribution and elevation of sight records, in conjunction with the distribution of apparently suitable forest habitat, we calculated the total area presently occupied. Kalij Pheasants now occupy approximately 3500 km^2, or one third of the total island area.

Food.—We recovered a number of food items from crops and gizzards of Kalij (Table 1). The omnivorous nature of their diet is evident; however, plant materials comprise the bulk of their food and include fruit, seeds, leaves, flower buds, and starch from trunks of tree fern (*Cibotium* sp.). In addition to the 19 plant foods identified, Kalij were seen feeding on fruits of 'olapa (*Cheirodendron trigynum*), 'ohelo (*Vaccinium reticulatum*), manono (*Gouldia terminalis*), pilo (*Coprosma* sp.), hame (*Antidesma platyphyllum*), and jacaranda (*Jacaranda acutifolia*). A wide variety of animal food was also identified, with preferred items mainly snails (Gastropoda), slugs (Gastropoda), and sowbugs (Isopoda), which were often seen on rotting fruits of banana poka (*Passiflora mollissima*), the birds' main food item. Kalij also consume a wide variety of larval and adult insects, earthworms, and even bird eggs.

Kalij obtain food with their stout bill by overturning small rocks, and pushing them backward toward their feet; digging into hard or moist soil to obtain invertebrates; pecking at the soil surface for seeds or fallen fruit; plucking seeds or buds from small forbs; or, by feeding on fruit in shrubs

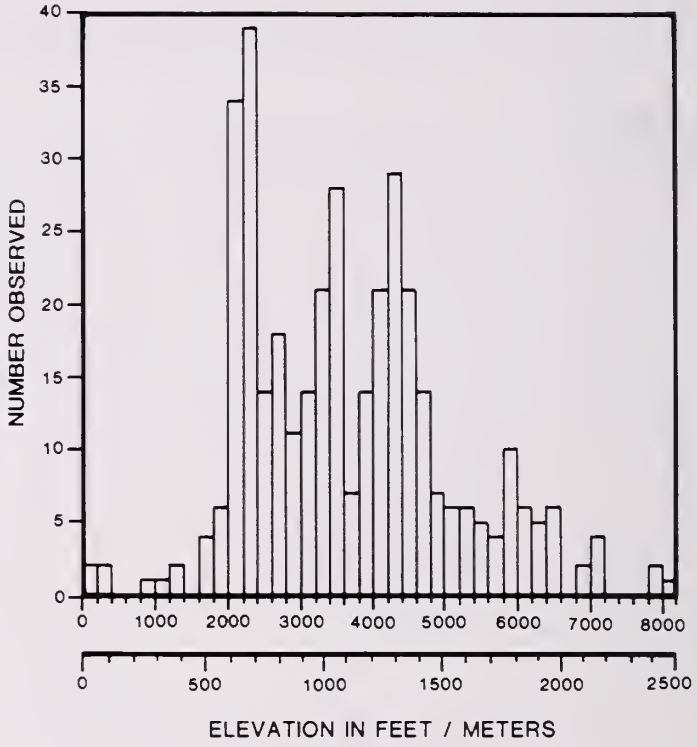

FIG. 2. Elevational distribution of Kalij Pheasants on the Island of Hawaii.

or trees. They are attracted to newly disturbed areas and are known to forage in the vicinity of tree cutting or tree fern harvesting operations within a half hour after the workers have left the area. Both pigs and Kalij forage in these disturbed areas for soil invertebrates and tree fern starch.

Fully 63% of the plant and 83% of the main animal food (gastropods and isopods) taken by Kalij are exotic species. The primary food of this pheasant is banana poka; 82% of the birds collected contained seeds and fleshy fruit of this vine. The exotic banana poka is regarded as the most important plant pest species in Hawaii (Warshauer et al. 1983). Thimbleberry (*Rubus rosaefolius*), another exotic pest, occurred in 36% of these pheasants. It was not uncommon to recover more than 100 banana poka seeds and several thousand thimbleberry seeds from a single gizzard.

Not all seeds are broken down by the grinding action of the grit in the gizzard, and many, apparently unharmed thimbleberry and banana poka seeds, occurred in the large intestine and feces. A germination test using

TABLE 1

FOOD ITEMS FROM CROPS AND GIZZARDS OF KALIJ PHEASANTS FROM HAWAII ISLAND

Food items	Status	% occurrence
Plant foods		
Banana poka (*Passiflora mollissima*)	exotic	81.8
Thimbleberry, 'ola'a (*Rubus rosaefolius*)	exotic	36.4
Tree fern, hapu'u (*Cibotium* sp.)	native	34.1
Gosmore (*Hypochoeris radicata*)	exotic	25.0
'Ihi (*Oxalis corniculata*)	exotic	18.2
Guava, kuawa (*Psidium guajava*)	exotic	18.2
Pukiawe (*Styphelia tameiameiae*)	native	18.2
Kikuyu grass (*Pennisetum clandestinum*)	exotic	15.9
Hawaiian raspberry, 'akala (*Rubus hawaiiensis*)	native	13.6
Poha (*Physalis peruviana*)	exotic	13.6
Passion fruit, liliko'i (*Passiflora edulis*)	exotic	9.1
'Ohelo (*Vaccinium calycinum*)	native	6.8
Drymaria, pipili (*Drymaria cordata*)	exotic	6.8
Misteltoe, hulumoa (*Korthalsella complanata*)	native	2.3
Candlenut tree, kukui (*Aleurites moluccana*)	exotic	2.3
Cassia (*Cassia bicapsularis*)	exotic	2.3
Air plant (*Kalanchoe pinnata*)	exotic	2.3
Cyanea, haha (*Cyanea pilosa*)	native	2.3
Holly, kawa'u (*Ilex anomala*)	native	2.3
Unidentified (seeds from 11 species, bulbs of one species)		2.3–11.4
Animal foods		
Gastropoda		
Small snail (*Oxychilus alliarius*)	exotic	31.8
Small slug (*Arion* sp.)	exotic	20.5
Large slug (*Limax maximus*)	exotic	18.2
Small snails (*Succinea* or *Catinella* spp.)	native	11.4
Large snail (*Bradybaena similaris*)	exotic	2.3
Isopoda		
Sow bug (*Porcellio* sp.)	exotic	18.2
Insecta		
Beetles, Coleoptera		11.4
Ants, Hymenoptera		2.3
Fly larvae, Diptera		2.3
Grasshoppers, Orthoptera		2.3
Butterfly larvae, Lepidoptera		2.3
Annelida		
Earthworm, Oligochaeta		2.3
Aves		
Bird egg shells		4.5

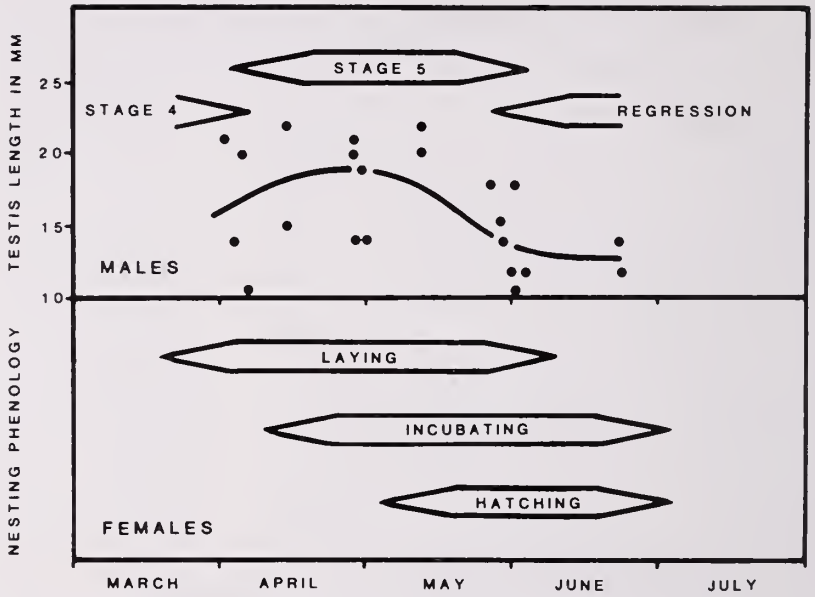

FIG. 3. Nesting phenology and testes size of Kalij Pheasants on the Island of Hawaii. The curve of average testes length is hand fitted to the data.

400 thimbleberry seeds kept on moist filter paper in petri dishes resulted in only one germinated seed. However, since large numbers are normally present in Kalij droppings, it seems likely that this bird might serve to disseminate viable exotic plant material via the intestinal tract. Apparently Kalij are also able to disseminate seeds or fruit attached to their feathers as five achenes of *Uncinea uncinata,* an endemic sedge, were found adhered to feathers of one bird's head and neck region.

Kalij use pieces of lava 2–10 mm in diameter as gizzard grit; however, the amount found was highly variable and ranged from 2–300 pieces. The gizzard also contained a variable number of hard seeds (range 0–472) which were usually banana poka, but some were from guava (*Psidium guajava*). Many of these seeds, especially banana poka, had been retained in the gizzard for sufficient time to erode, as the hard outer surface was worn revealing the characteristic pitted layer. By using regression correlation of log-log transformed data we compared the relationship between the number of lava rocks in the gizzard to the number of hard seeds, and found a highly significant negative relationship ($r = -0.612$, $df = 40$, $P < 0.01$). Thus, it appears that Kalij not only use the fruits of these two exotic plants for food, but also retain their hard seeds as gizzard grit.

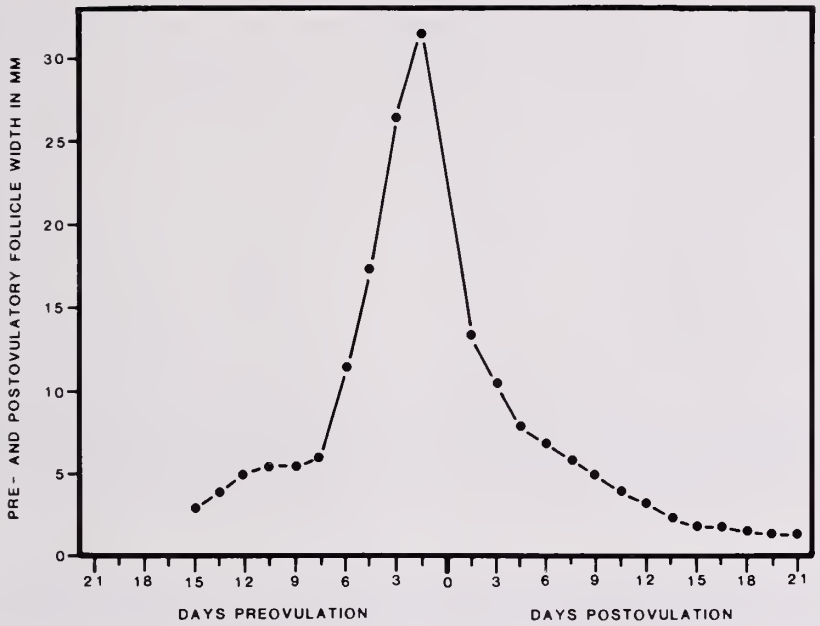

FIG. 4. The growth of the ova and regression of the residual ovarian follicle of Kalij Pheasants.

Reproduction.—Maximum testes growth, to slightly over 20 mm, is achieved by late March, and most males retain fully functional testes throughout April and early May (Fig. 3). During this time the seminiferous tubules are in the stage 5 condition, i.e., maximum numbers of spermatoza are being produced. In late May testes enter the regression stage, and by mid-June are at the overwintering length of about 10 mm.

Examination of the ovarian follicles revealed that laying occurred between mid-March and mid-June. By observing the number and size of both pre- and postovulatory follicles, we estimated that these pheasants lay from 10–17 eggs. Ova develop slowly, until about a week prior to laying, then undergo rapid growth and ovulate at a diameter of about 30 mm (Fig. 4). The remaining follicle undergoes resorption and reaches the minimum size in about 2 weeks. This curve may be used to predict the date of ovulation of any developing ovum or to postdate when any postovulatory follicle had ovulated its ovum. Thus, reproductive phenology of this pheasant may be determined by gross examination of female ovarian tissue between the beginning of March and the end of June. Additionally, if the inter-egg interval is 1.5 days and the incubation period is

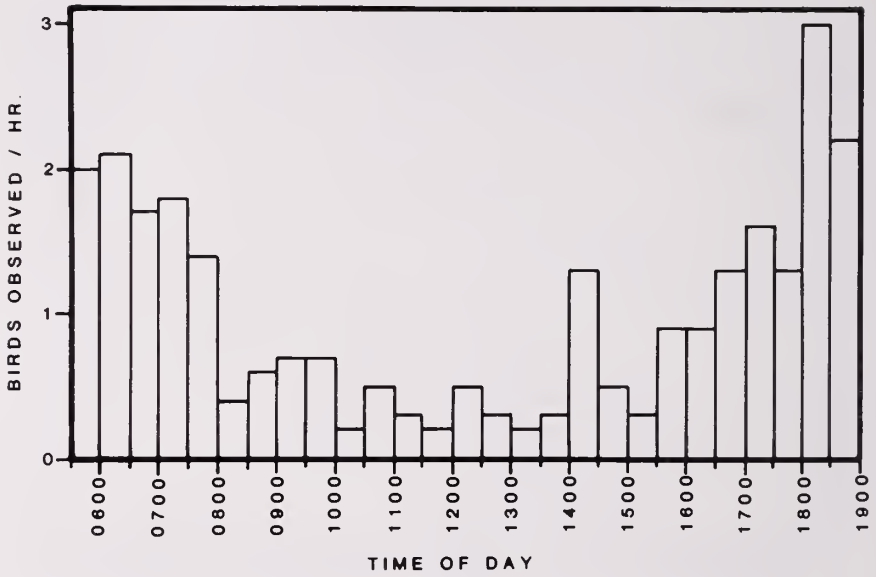

FIG. 5. Daily activity pattern of Kalij Pheasants on the Island of Hawaii between January and June 1981.

24 days (Delacour 1977) then a Kalij hen would take 21 days to lay 10–17 ($\bar{x}$ = 14) eggs and the chicks would hatch 45 days after the first egg was layed. The hatching period for the Hawaiian population was estimated to occur between the first week of May through the first week of July (Fig. 3). The testes and ovaries of all adult pheasants examined were fully functional indicating that all members of this population were capable of breeding as yearlings.

Behavior.—Kalij Pheasants had early morning and late afternoon peaks of foraging with lower levels at mid-day (Fig. 5). This is a typical activity pattern of most game birds. Kalij emerge from the forest at dawn and are particularly attracted to clearings or disturbed areas such as trails, roads, logging areas, and forest clearings. The practice of leaving log piles in newly cleared pasture adjacent to native forest is particularly attractive to these pheasants since they not only use the abundant new crop of exotic forbs but also use the log piles as escape cover. Kalij forage in pasture edges around these piles up to 100 m from thick forest cover.

During the breeding season the female almost always leads her mate by a few meters as they search for food. However, this activity is occasionally interrupted by three common behavioral patterns. "Wing-fluttering" is usually performed by the cock and consists of 8–10 rapid strokes

TABLE 2
SOCIAL ORGANIZATION AND SEX RATIO OF KALIJ PHEASANTS

Associations	Observations		Sex ratio males/females
	No.	%	
♂♀	49	39.2	49/49
♂	37	29.6	37/0
♀	16	12.8	0/16
♂♂♀	6	4.8	12/6
♂♂	4	3.2	8/0
♂♀♀	1	0.8	1/2
♀ + chicks	3	2.4	0/3
♂♀ + chicks	2	1.6	2/2
♂ + chicks	1	0.8	1/0
Sex undetermined	6	4.8	—
Totals	125		110/78 = 1.4 ♂♂/1.0 ♀♀

of half extended wings performed while the body is in an upright posture. It may be repeated up to four times with 30 sec intervals. It was primarily given by mated males but was seen occasionally in lone males and was observed once performed by a hen. It was mainly performed near the hen but in only half of the cases was the cock facing his mate. A male wing-fluttered towards us on one occasion as we closely approached a mated pair. Wing-fluttering may serve to facilitate pair bonding and also serve as a distraction or alarm display.

We observed the "run-jump" display to be performed only by mated males and was directed toward the hen. A male runs toward the hen from several meters ending the approach with up to four jumps, then turns away from her at a distance of 1 m. If this is performed with greater intensity, the male runs, then jumps toward his mate, circles her twice, then may perform a wing-flutter, but does not necessarily face her.

The "tail-fanning" display is also performed by mated cocks which run several meters toward their mate, to within 1 m, then turn sideways and fan their long, black tail feathers. The pair immediately resumed feeding following all of these displays.

Social structure.—The breeding associations of Kalij Pheasants in their native areas are unknown (Ali and Ripley 1969, Delacour 1977). In Hawaii, mated pairs were observed more often (41%) than any of the other sexual combinations (Table 2). We did note one case involving a male who was seen copulating with a hen while another hen stood immediately beside them. Ali and Ripley (1969) described an observation of a cock

with two hens and a brood of chicks. Monogamy may therefore be the rule in Kalij, with polygamy the exception.

Chicks can be cared for by the mated pair or by either sex alone. Lone cocks will apparently even brood small chicks as we observed a cock walk out of low, wet grass during a rain storm to reveal a brood of dry, downy chicks.

We were able to sex all but 6 of our 194 adult sightings. The sex ratio of these birds was 141 males/100 females. The excess number of males supports the alleged monogamous breeding system.

DISCUSSION

The successful colonization of Hawaii island by Kalij Pheasants can be thought of as a symptom of a degraded ecosystem, because the birds are in large measure dependent on both exotic plants and animals for food and cover. The birds are still rapidly expanding their range and we believe their colonization of this island is not yet complete. The three remaining uninhabited areas (central Kau and Puna forests, and Kohala Mountain), will probably shortly be colonized. It appears that the success of this species will prompt its transplantation to other areas on Hawaii, and possibly to other islands. Kalij apparently have the ability to enhance the establishment of exotic plant pests, and may act as a predator on rare endemic land snails. It is for these reasons, as well as their potential as disease reservoirs (Lewin and Mahrt 1983), that extreme caution is advised prior to transplantation. Certainly, stock should be obtained from areas free of banana poka.

SUMMARY

The colonization of the Island of Hawaii by the Kalij Pheasant (*Lophura leucomelana*) is described. This Himalayan game bird, released in 1962 at Puu Waawaa, has spread at the rate of about 8 km/year and now occupies most of the major forest areas between 450 and 2150 m elev. This population constitutes a new wild breeding species of game bird for the Western Hemisphere. The bird is omnivorous and relies heavily on exotic plants and animals. Their main food item is banana poka (*Passiflora mollissima*) which provides fruit as well as seeds for grit. The Kalij may play a role in seed dissemination of pest plants. The Kalij is mainly monogamous and yearlings can breed. Laying begins in mid-March and hatching terminates by mid-July. Daily activity patterns including foraging, pair bonding, and alarm behavior are described. Due to the potential for dissemination of exotic pests and possible impact on endemic biota, caution is advised on the inter-island transplanting of this exotic game bird.

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GEORGE MIKSCH SUTTON AWARD FOR ORNITHOLOGICAL ART

The Wilson Ornithological Society announces the establishment of the George Miksch Sutton Award for Ornithological Art. The Award will be given for art that would be suitable as a color plate in The Wilson Bulletin. The subject matter and medium are at the artist's discretion. Size of the artwork should be no smaller than 9¼ wide × 14 inches high and no larger than 18⅜ × 27¾. Any artist who has not been represented by a major gallery or who has not been featured in magazines such as Audubon or National Wildlife is eligible to enter. Prior publication of a color plate in a professional journal does not disqualify an artist. In short, the competition is primarily for artists who do not make their living, or a significant portion of it, by painting birds. Artists who question their eligibility should query the Award Committee when requesting entry information. Artwork will be judged by a panel of ornithologists and artists at the June 1985 Wilson Ornithological Society/Cooper Ornithological Society joint annual meeting in Boulder, Colorado. All qualified entries will be on display at the meeting. Artists should insure their entries both to and from the meeting and include a return mailer with postage attached. Matting and/or framing is at the discretion of the artist. The winner of the competition will receive a check for $500, and his/her artwork will appear as a color plate in The Wilson Bulletin. For further information and application form, contact **Phillips B. Street, Chairman, Sutton Award Committee, Lionville Station Road, R. D. 1, Chester Springs, Pa. 19425.**

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DIFFERENTIAL RANGE EXPANSION AND POPULATION GROWTH OF BULBULS IN HAWAII

Richard N. Williams and L. Val Giddings

The Red-whiskered Bulbul (*Pycnonotus jocosus*) and the Red-vented Bulbul (*P. cafer bengalensis*) on Oahu, Hawaii, present a unique natural experiment in colonization rates. Both species were introduced on Oahu in the mid-1960s and are currently undergoing rapid population growth; however, they differ markedly in rates of range expansion. Van Riper et al. (1979) reviewed the range and population growth of the two species through 1977 and found the red-whiskered restricted to a small area in central Honolulu while the red-vented was distributed throughout lower elevation habitats in the southeast quarter of Oahu. The objectives of our study were: (1) to document continued range expansion and population growth by both species; and (2) to determine if differences in their rates of range expansion could be attributed to differing rates of population growth or differences in habitat selection. Here we report on a marked range expansion by the Red-vented Bulbul and continued rapid population growth by both species and suggest several hypotheses (currently under investigation) to explain the marked differences in distribution and habitat selection between the two species.

Red-whiskered and Red-vented bulbuls were introduced to Oahu without legal authorization in 1965 and 1966, respectively (Berger 1975, Williams 1983). Both species are native to India where they inhabit gardens, scrub, second growth, forest edges, and agricultural areas (Ali and Ripley 1971). They are similar in their morphology and ecology, including nesting and feeding habits (Ali and Ripley 1971). Both species appear preadapted for living in the residential lowlands of Oahu, many areas of which are replete with exotic fruit-bearing trees (Neal 1965).

Bulbuls have demonstrated the ability to colonize after being introduced in a number of temperate, tropical, and subtropical habitats. The red-whiskered is established in southeastern Australia (Long 1968), Mauritius (Long 1981), California (Hardy 1973), and Florida (Carleton and Owre 1975), while the red-vented is found in Fiji (Watling 1978), Tahiti (Bruner 1979), Tonga (Dhondt 1976a), Western Samoa (Dhondt 1976b), and southeastern Australia (Slater 1974). In most of these areas, they are considered pest species due to agricultural crop damage or as vectors for the dispersal of weedy plant species (Watling 1977). For these reasons,

the ecology, distribution, and population growth of the bulbuls in Hawaii are of both scientific and practical interest.

METHODS

We conducted an intensive survey (134 h of observation) from July 1981–February 1982, to document the current distribution of bulbuls on Oahu and conducted periodic surveys (46 h) through the remainder of 1982 to document any subsequent range expansion. We concentrated our surveys in areas below 200 m elevation along Oahu's coastal perimeter and central valley in residential, forest, and agricultural lands. We made some observations in second growth and native forests above 200 m. We recorded time (in min) at each survey location from the start of observations until the first bulbul of each species was detected. Elapsed observation time until detection was assumed in this study to reflect relative abundances. Elapsed observation times shown in Figs. 1 and 2 are average values, as data were collected more than once (range 2–6) at each location.

We examined population growth with data from the Hawaii Audubon Society's annual Christimas Bird Counts for the Honolulu area (Pyle 1965–1982). The Honolulu Count circle covers 456 km^2, including and extending beyond the introduction sites for both species. In order to standardize count results over the years 1965–1982, total number of bulbuls observed each year (by species) was divided by total party hours for that same year. As population growth is typically exponential, natural log transformations were performed on standardized population values for the Red-whiskered Bulbul from 1974–1982, and for the Red-vented Bulbul from 1968–1982, as these periods represent continuous growth intervals for these species. Population growth rates (regression coefficients) were examined for homogeneity using Homogeneity of Slopes model ANOVA (SAS 1982).

We examined distributional patterns of bulbuls in residential Honolulu throughout Manoa and Nuuanu valleys where both species were found in the highest concentrations. We started transects (5.0 km in length) in the upper valleys and extended them down past the valley mouths such that the upper half of the transect in each valley was located at higher elevations and received greater rainfall than did the lower half. Each transect was subdivided into 100-m segments, giving 50 segments per transect. Data were collected monthly from each transect with numbers of either species recorded for every 100-m segment. Odd-numbered segments were censused during odd-numbered months and even-numbered segments during even-numbered months. All observations were made during the first 3.5 h after sunrise. Thus, data were recorded for twenty-five, 100-m segments on each transect each month. Transect data were anlysed using Chi-square procedures to test within species differences in number of birds observed in the upper and lower halves of each transect (Little and Hills 1978). Significant differences ($P < 0.05$) were assumed to reflect habitat preferences for wet exotic residential habitat (upper half of transect) or dry exotic residential habitat (lower half of transect).

RESULTS

The distribution of the Red-whiskered Bulbul on Oahu is restricted to the central Honolulu area where there are two known introduction sites (Fig. 1) (Williams 1983). Red-whiskereds were found in low concentrations throughout most of their Oahu range. Highest concentrations were observed in residential areas in the upper portions of Manoa and Nuuanu valleys. Results from our intensive survey in 1981 and early 1982, showed a distribution almost identical to 1977 (Fig. 1). Periodic surveys through-

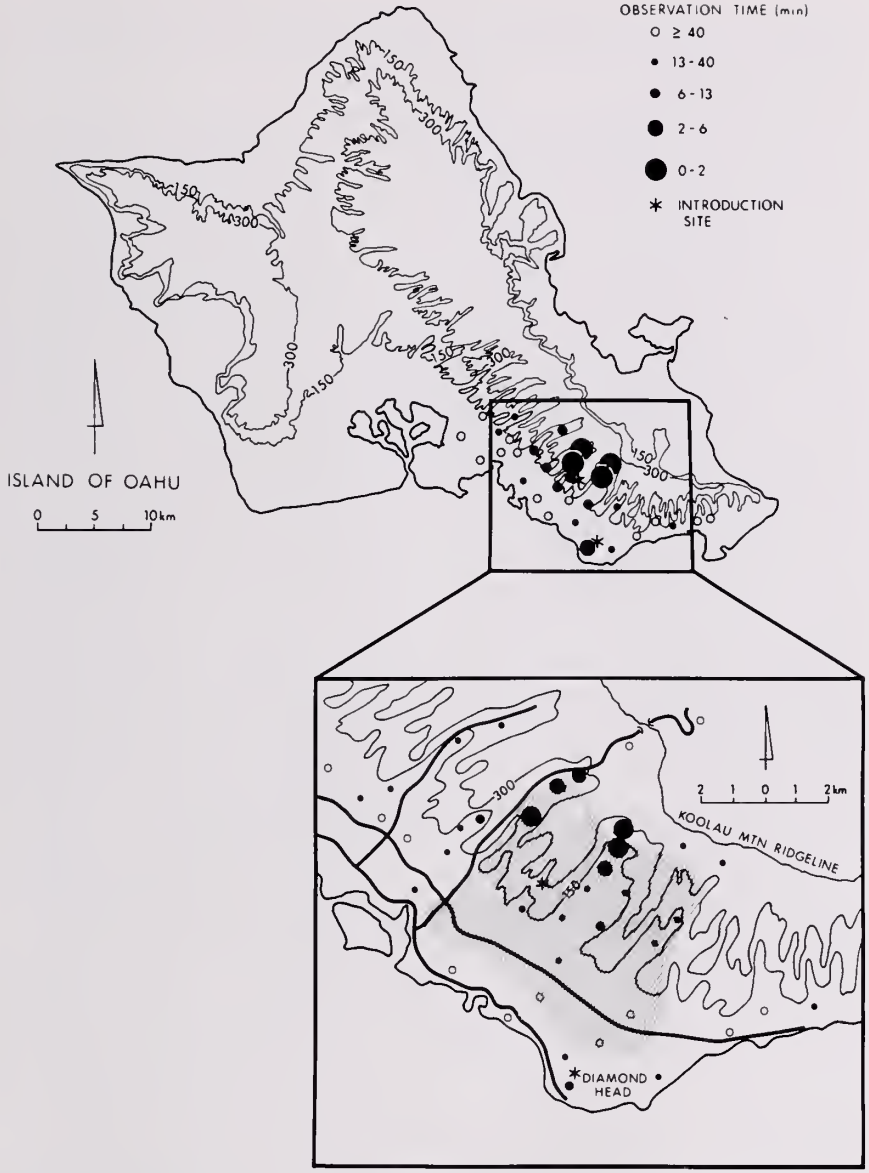

FIG. 1. Distribution and abundance of Red-whiskered Bulbuls on Oahu and in central Honolulu (inset map) as of December 1982. Open and closed circles indicate absence or presence of bulbuls, respectively. The larger the circle, the greater the relative abundance and the shorter the elapsed observation time. Data values on upper map are summary values, whereas values on inset map are actual data values from each location. Shaded section denotes 1977 distribution as reported by van Riper et al. (1979). Contour lines depict elevation in meters.

out the remainder of 1982 defined a larger distribution; one in which red-whiskered densities were quite low in areas lying outside the limits of the 1977 distribution.

In contrast to the limited distribution of the red-whiskered, we observed red-venteds at most lower elevations (Fig. 2). In 1977, the red-vented was restricted to the southeast quarter of Oahu, a distribution that encompassed the locations where it was first observed on Oahu in 1966–1967 (Williams 1983). The 1981–1982 survey revealed an absence of Red-vented Bulbuls on the western coast of Oahu. In August 1982, we discovered a small group in the lowland central portion of Makaha Valley. Since that time, we have made additional observations of this species along the western coast, although the birds are present in very low numbers. Numbers of red-venteds increased moving inland from the coast (Fig. 2 inset), reaching their highest levels in mid-elevation (100–200 m) portions of Honolulu's residential areas. They decreased in upper residential areas and wet exotic forest at elevations above 200 m.

We tested the hypothesis that the differences in distributions between the red-whiskered and the red-vented might be attributable to differential rates of population growth. The red-whiskered was first recorded in the 1967 Honolulu Area Christmas Bird Count and the red-vented in the 1968 count. Population growth through 1982 for both species is shown in Fig. 3. Population growth rates (regression coefficients) were 0.493 for the red-whiskered and 0.383 for the red-vented. Since the data were logarithmically transformed, these rates represent population doubling times of 1.4 and 1.8 years, respectively. Population growth rates were tested for homogeneity and there was no significant difference ($P > 0.05$).

To test for differences in habitat preference between the two species, we examined distributional patterns of bulbuls in residential Honolulu using monthly transet censuses over a 12-month period (Table 1). Red-whiskered Bulbuls were counted in significantly greater numbers ($P < 0.05$) in the upper half of Manoa Valley during 9 of 12 months of observations and in the upper half of Nuuanu Valley during 10 of 12 months. Significant differences were not detected for either species in Manoa Valley in November or December of 1982 during the non-breeding period for both species. By contrast, the red-vented occurred in significantly greater numbers ($P < 0.05$) in the lower half of Manoa Valley during 9 of 12 months. Red-vented distribution in Nuuanu was not significantly different ($P > 0.05$) in 11 of 12 months. Only in February 1983, were significantly more individuals ($P < 0.05$) detected in the lower half of the transect. Comparisons between Manoa and Nuuanu showed approximately equal numbers of red-venteds in the upper half of each transect (279 and 276

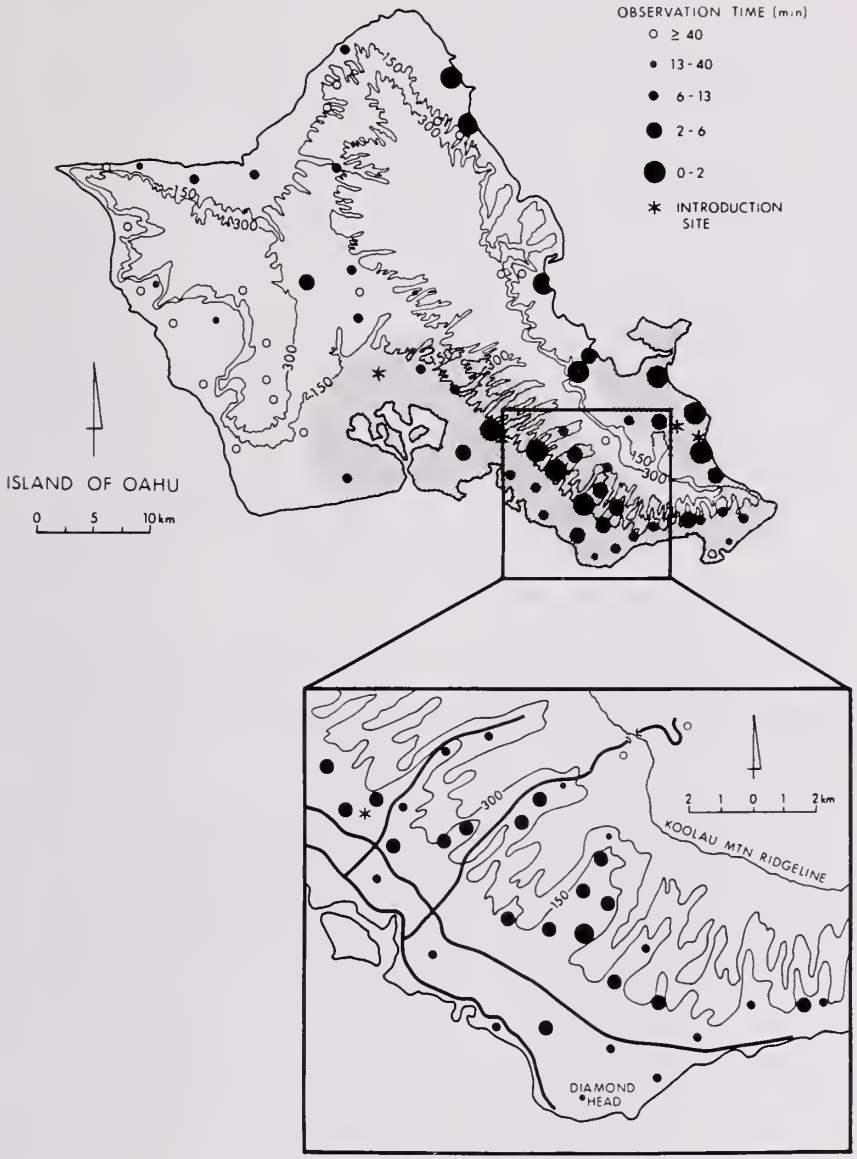

FIG. 2. Distribution and abundance of Red-vented Bulbuls on Oahu and in central Honolulu (inset map) as of December 1982 (symbols as in Fig. 1).

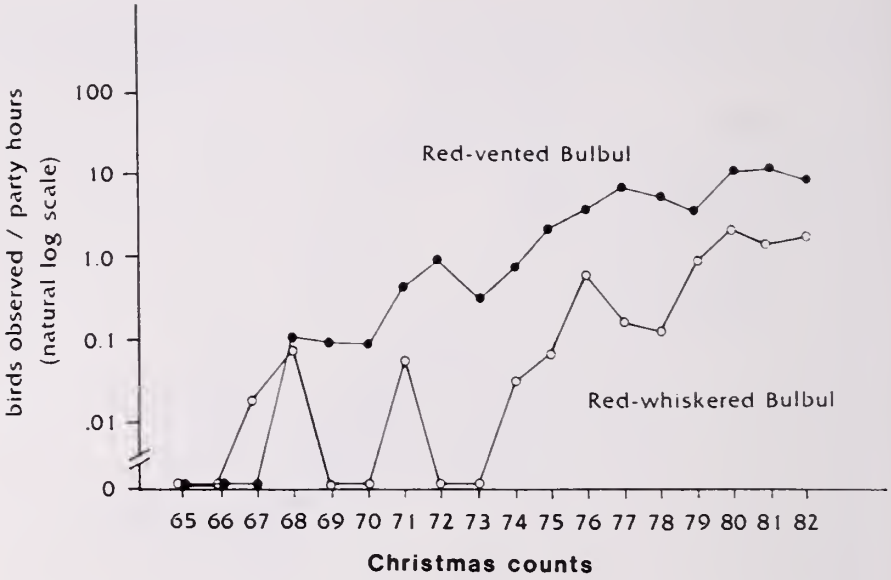

FIG. 3. Population growth of bulbuls on Oahu, 1965–1982. Data from Honolulu Christmas Bird Counts (Pyle 1965–1982).

birds, respectively), yet twice as many in the lower half of Manoa (546) as Nuuanu (268) ($\chi^2 = 86.4$, df = 1, $P \leq 0.05$).

DISCUSSION

As described above, we were intrigued by differences in range expansion rates and distribution of the two species. We hypothesized that the red-vented had a much higher rate of population growth than the red-whiskered, and that as the population grew, dispersal and subsequent range expansion accounted for its more extensive distribution. This hypothesis was tested using data from the Honolulu Area Christmas Bird Counts and was rejected by two results. First, the regression coefficients representing rates of population increase for the red-whiskereds and red-venteds did not differ significantly. Second, from 1977–1982, the red-vented approximately tripled its range on Oahu while the red-whiskered maintained a distribution similar to that defined in 1977 by van Riper et al. (1979). Therefore, it appears that differences in distribution and rate of range expansion between the two bulbuls cannot be ascribed to differences in population growth rates.

Differences in the distributions of the Red-whiskered Bulbul and the Red-vented Bulbul on Oahu suggest that they may be selecting differing habitats. In India, these two species have demonstrated habitat parti-

TABLE 1

NUMBERS OF BULBULS OBSERVED IN UPPER (U) AND LOWER (L) HALVES OF TRANSECTS IN MANOA AND NUUANU VALLEYS, OAHU, JUNE 1982–MAY 1983

	Months											
	1982							1983				
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Manoa Valley												
Red-whiskered	U32*	47*	34*	56*	34*	15	13	25*	27	19*	11*	8
	L11	4	12	16	11	11	9	10	18	7	3	10
Red-vented	33*	36*	32*	51	10*	20	18	15*	13*	16*	20*	14*
	95	68	73	43	32	28	22	31	35	38	35	44
Nuuanu Valley												
Red-whiskered	50*	17	25*	23	34*	25*	28*	32*	34*	27*	17*	22*
	12	18	10	21	13	4	9	6	7	8	5	8
Red-vented	34	30	20	17	36	18	23	18	19*	23	20	18
	29	18	16	14	23	26	24	18	39	21	27	15

* $P < 0.05$.

tioning within their native ranges (Ali and Ripley 1971). Vijayan (1975) examined their ecological isolation in India and concluded that distributional patterns were determined by habitat characteristics. According to those authors, distributions of red-whiskereds and red-venteds in India exhibited a high degree of overlap, with both species occurring in agricultural and residential areas and in scrub jungle. However, the red-whiskered was found predominantly in wet habitats from 500–2000 m elevation, whereas the red-vented occurred predominantly in dry habitats from sea level to 1500 m.

Based on the above discussion and on observations made during our initial surveys of bulbul distributions on Oahu, we generated two hypotheses. These were: (1) the Red-whiskered Bulbul occurs predominantly in the upper wet portions of Manoa and Nuuanu valleys; and (2) the Red-vented Bulbul occurs predominantly in lower elevation, drier habitats near the mouths of Manoa and Nuuanu valleys. We tested these hypotheses, using data from the monthly transect censuses in Manoa and Nuuanu valleys.

Bulbuls on Oahu demonstrated habitat preferences similar to bulbuls in India and these differences may be responsible for their present distributions. Census results from the transects confirmed that the Red-whiskered Bulbul occurred predominantly in the wet upper residential portions of Manoa and Nuuanu valleys. However, the few observations from the wet exotic forest above the transect included few or no red-

whiskereds. These observations need further corroboration (and are under continuing investigation), but suggest that red-whiskered densities decreased rapidly in all directions outward from the wet urban residential habitat in upper Manoa and Nuuanu valleys. Therefore, the preferred wet exotic residential habitat of red-whiskereds can be viewed as occurring on Oahu in a series of disjunct patches located at the heads of leeward valleys. Consequently, range expansion by the red-whiskered on Oahu has probably been impeded by difficulty in dispersal and colonization between habitat patches in the valley heads.

As predicted, the Red-vented Bulbul occurred predominantly in the lower half of Manoa Valley in drier habitats; however, in Nuuanu Valley, numbers of birds observed in the upper and lower halves of the transect did not differ significantly ($P > 0.05$). Results of the initial distribution survey and the transect counts showed a continuous distribution of the Red-vented Bulbul throughout residential portions of central Honolulu. Highest concentrations were observed in areas at low elevations, such as lower Manoa Valley, the Fort Shafter area, and along the windward (northeast) coast. Although Red-vented Bulbuls were abundant in agricultural, residential, and kiawe (*Prosopis pallida*) scrub habitats along the north, east, and south coasts and throughout the central valley (see Fig. 2), their numbers decreased rapidly as one progressed up into the Koolau Mountains (Shallenberger 1978, this study) or the Waianae Mountains (this study).

High concentrations of red-venteds on Oahu were continuous, that is, they were not separated by areas of low concentration as were those of the red-whiskered. The highest numbers of red-venteds occurred in the lower elevations and drier portions of all valleys throughout Honolulu and along the windward coast. These habitats form a continuous belt around the perimeter of Oahu and through the center of the island, and thus have apparently served as a corridor for dispersal and range expansion of the Red-vented Bulbul on Oahu.

SUMMARY

Population growth and distributional patterns of Red-whiskered (*Pycnonotus jocosus*) and Red-vented (*P. cafer bengalensis*) bulbuls were examined from their introductions to Oahu in the mid-1960s to the present. Population growth rates for the two species did not differ significantly ($P > 0.05$). The red-whiskered was observed only in the central Honolulu area, primarily in wet, exotic, residential habitats above 150 m elevation; whereas, the red-vented was observed in most habitats below 200 m island-wide. These observed differences in habitat preference were quantified and found to differ significantly ($P < 0.05$) using 12 monthly transect censuses in Manoa and Nuuanu valleys. Differences in the distributions of the two bulbuls can be explained as a result of differences in habitat preference. The wet, exotic, residential habitat preferred by the red-whiskered is of restricted size and occurs in disjunct patches, thus limiting the spread of the Red-whiskered Bulbul across Oahu. Lower

elevation, drier habitats form a continuous belt around the perimeter of Oahu and through the center of the island and thus, have apparently served as a corridor for dispersal and range expansion of the Red-vented Bulbul on Oahu.

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BEHAVIORAL AND VOCAL AFFINITIES OF THE AFRICAN BLACK OYSTERCATCHER (*HAEMATOPUS MOQUINI*)

ALLAN J. BAKER AND P. A. R. HOCKEY

The African Black Oystercatcher (*Haematopus moquini*) is endemic to southern Africa, occurring as a breeding species from the Hoanib River mouth in Namibia around the Cape of Good Hope to Mazeppa Bay, Transkei (Hockey 1983a, S. Braine, in litt.). *H. moquini* has wholly melanistic plumage and, like other Old World species, adults have scarlet irides, bright coral-pink legs and jet-black feathers on the back. Its systematic relationships are problematical, some authorities (e.g., Peters 1934; Larsen 1957) preferring to treat it as a subspecies of the European Oystercatcher (*H. ostralegus*), whereas others accord it full species status (e.g., Heppleston 1973; Clancey 1980).

Recent studies have revealed details of the general biology of *H. moquini* (Summers and Cooper 1977; Hockey and Cooper 1980; Hockey 1981a, b, 1982, 1983a, b, c, 1984; Hockey and Branch 1983, 1984; Hockey and Underhill 1984). Despite this wealth of ecological knowledge, the only report of the breeding behavior of this species is that of Hall (1959), which is based on relatively few birds and does not cover the repertoire of known behaviors of oystercatchers (see Makkink 1942, Williamson 1943, Miller and Baker 1980). Vocalizations of *H. moquini* have not been studied previously. In this paper we describe the behavior and vocalizations of African Black Oystercatchers during the breeding season in the southwestern Cape Province, South Africa. Our ultimate goal is to provide comparative data to assist in clarifying relationships within the Haematopodidae (Baker 1974, 1975, 1977).

METHODS

Observations of *H. moquini* were made principally during the breeding season early in 1982 (January 6–8, 13–15, and 20–24) at Marcus Island (33°02′S, 17°58′E) and Malgas Island (33°03′S, 17°55′E) in Saldanha Bay, southwestern Cape Province, South Africa. General observations on the behavior of birds on these sites in 1979 and 1980 were made by the second author. Motion pictures of displays were taken with an Elmo super 8 mm sound camera at 24 frames/sec to ensure good sound fidelity. Behavioral interactions among three territorial pairs were filmed from a portable canvas hide located within 20 m of the birds. Displays of birds with young were filmed at close range (ca 5–20 m) with the observers in full view. Figures of various displays were prepared by tracing images from still-frame projections. Descriptions of all display behaviors are based on terminology suggested by Cramp et al. (1983).

Tape recordings of all vocalizations were made at 19 cm/sec on a Uher 4200 Report Stereo IC tape recorder using Scotch 177 tape and a Dan Gibson parabolic reflector (model P-200) and microphone. Tapes were analyzed with a Unigon FFT Spectrum Analyzer and sonagrams and amplitude envelopes of vocalizations were prepared using a Kay Elemetrics Digital Sona-Graph 7800 set on a wide band filter (300 Hz) and the 80–8000 Hz range.

Whenever possible the sex of the displaying birds was recorded. At Marcus Island almost all birds had previously been color-banded with unique combinations of bands, and were sexed at the time of capture by the degree of distension of the cloaca. Females have visibly distended cloacas for up to 10 days after laying is completed (Hockey 1981b). Unbanded birds usually could be sexed by direct observation in "backlighting" views because the base of the bills of females is orange whereas in males it is reddish-orange, as has been noted for other species of oystercatchers (Miller and Baker 1980). Additionally, within pairs males of *H. moquini* commonly have a shorter and less pointed bill than their respective mates (Hockey 1981b).

BEHAVIOR

Copulation.—The only filmed sequence of copulation we obtained for *H. moquini* revealed specific posturing by both members of a pair. The female solicited copulation by assuming a stationary pre-copulatory posture in which she inclined her body forwards and pointed her head and bill downwards at about 45° to the ground. The male responded by approaching his mate from one side with the "stealthy walk" (Makkink 1942) in which his body was hunched noticeably, his head was drawn tightly into his breast, and the wings were raised slightly up and away from the body (Fig. 1A). Just before the male flew onto her back, the female crouched lower and raised and spread her folded wings outwards (Fig. 1B). The male balanced on the female by flapping his wings while sitting with his tarsi and feet along her back (Fig. 1C). Apparent cloacal contact was made by the male rotating his body backwards and downwards, and then arching his pelvic region forwards (Fig. 1D). The copulation was terminated soon after this when the female reached back and grasped the male's bill with her own, whereupon the male dismounted immediately (Fig. 1E–F).

On some occasions copulation was preceded by display behavior which closely resembled piping (see beyond). In this pre-copulatory display both birds of a pair walked forwards together with their bills held at an angle between 45° and 90° to the ground, after which copulation proceeded as described above. In the breeding season copulations were observed following the cessation of territorial disputes, aerial chases of intruding oystercatchers, and "butterfly flights." Copulations were also observed outside the breeding season from mid-winter (June and July) through early spring (near the end of August) when territorial interactions increased in frequency. Of 11 attempted copulations observed in winter and spring three

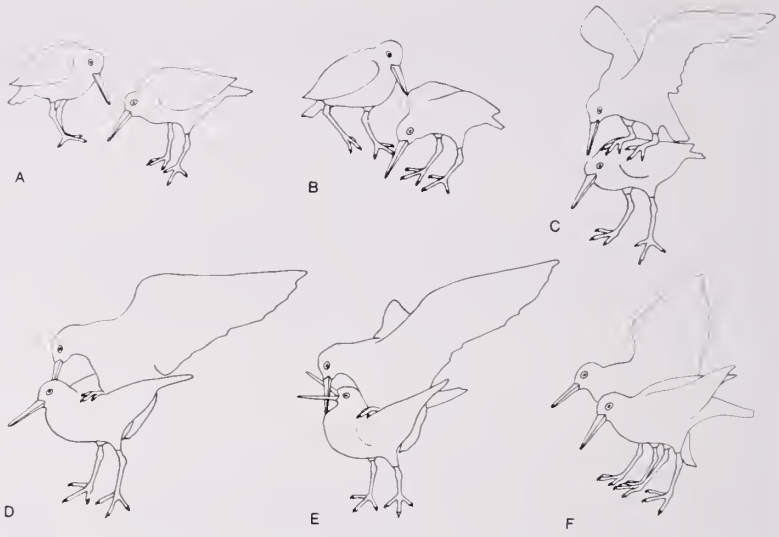

FIG. 1. Copulatory sequence (based on filmed sequence) by a pair of *H. moquini*. (See text for details).

did not culminate in cloacal contact, whereas all seven observed in the breeding season in January 1982 (when eggs were being laid on Marcus Island) were completed successfully. Copulations were brief, ranging in duration from 3–9 sec (mean duration ± SE = 5.9 ± 0.64 sec, N = 12).

Piping.—Piping displays on the ground were characterized by striking postures and vocalizations. A typical sequence of postures taken from one continuous piping display by a pair of birds when swooped on by a passing neighbor is shown in Fig. 2. In this example the male (Fig. 2A, right bird) began vocalizing while he held a posture in which the head was inclined downwards and forwards, the bill was almost vertical to the ground, and the wings were raised markedly at the carpal flexure and held away from the body. The female walked towards the male with the bill held vertically and began calling (Fig. 2B, left bird). She turned counterclockwise in this posture (Fig. 2C) and then performed a "parallel run" with her mate (Fig. 2D) covering a distance of approximately 15 m. Both birds halted at this point and turned to face each other, still continuing to vocalize loudly (Fig. 2E). Shortly thereafter the female stopped calling and stood upright (Fig. 2F), and then the male ceased calling too. Subsequently, he approached the female in a hunched pre-copulatory posture (Fig. 2G) and nudged her aside while performing "false-feeding" (Fig. 2H). Both birds concluded the display sequence by preening vigorously.

Piping displays were most frequent early in the breeding season when

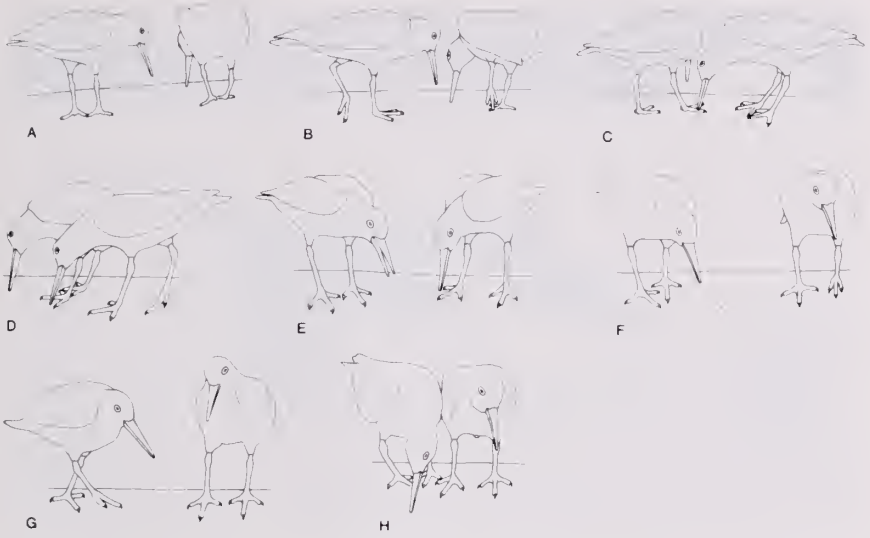

FIG. 2. Piping display sequence (based on filmed sequence) by a pair of *H. moquini*. (See text for details.)

birds were establishing and defending territorial boundaries. Intruders were usually repelled by mutual piping displays by both members of a pair, but when one bird was absent from the territory the remaining bird performed alone. As in other species of oystercatchers (see Miller and Baker 1980) piping displays in *H. moquini* were highly contagious, often attracting birds from nearby territories. The number of birds observed in piping groups varied from 2–17, but the usual number was three or four.

Groups piping on the ground sometimes wandered across several territories, but often they occurred in areas of suboptimal nesting and feeding habitat not occupied by territorial birds. Piping also occurred in flight when up to eight birds participated. Members of a pair piped in unison with their necks arched down and bills held vertically while flying in parallel formation, and this is clearly the aerial counterpart to parallel running on the ground. In both aerial and ground displays involving larger numbers of birds some of the participants adopted piping postures but remained silent. We never observed juveniles taking part in piping displays.

Distraction displays.—Breeding adults performed elaborate distraction displays in defence of young. One display, hereafter referred to as the distraction-lure display, has never been described for any species of oystercatchers (Fig. 3).

The high-intensiy form of the distraction-lure display was given re-

FIG. 3. Distraction-lure display of an adult *H. moquini*. Note the raised tail.

peatedly by parent birds (five of six displays were given by females) when we held their chicks in full view and especially when the chicks gave distress calls. All displays we filmed were very similar in that they were composed of sequences of exaggerated postures designed to attract attention to the displaying bird. In one such display the female responded to our presence by flying onto the top of a large rock within 5 m of our position, and then raised her folded wings asymmetrically away from the body while orienting directly towards us (Fig. 4A). At the same time she began calling rapidly. After holding this position for about 5 sec she then turned sideways on the same spot and began to slowly flap her wings (Fig. 4B). She gradually assumed a striking oblique posture by tilting her body forward so that the bill was at an angle of about 30° to the ground (Fig. 4C–E) and the tail was elevated slightly and alternately fanned and closed. About 22 sec later the female moved slowly away from us in a pronounced crouching posture while continuing to flap her wings (Fig. 4F). After jumping down from the rock to a wave-cut platform she broke into a slinking run (Fig. 4G) of about 20 m until she disappeared behind boulders. On several occasions the running bird crouched very low, arched its back, and depressed its tail (Fig. 4H) in a characteristic "crouch-run" (Cramp et al. 1983) before "hiding" in a crouched posture with the head and bill flattened along an exposed rocky crevice.

When we stood close to the hiding place of their chicks (without hand-

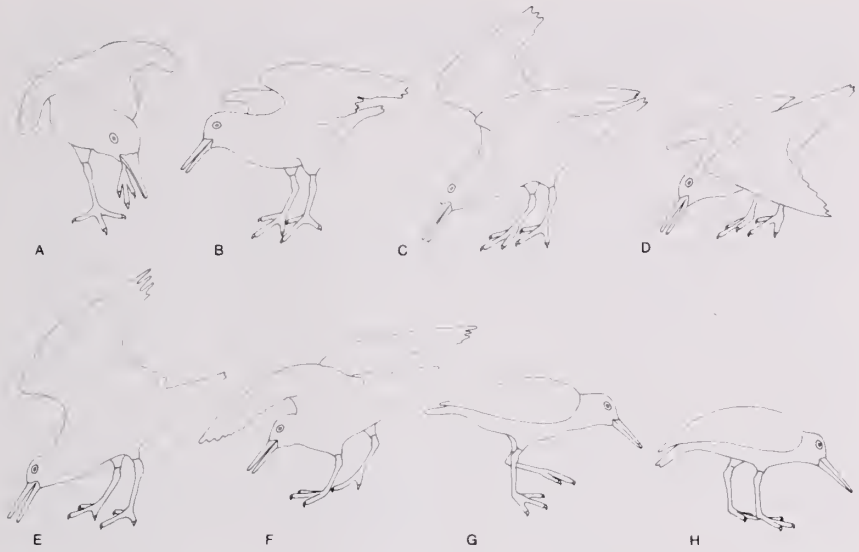

FIG. 4. Behavior of a female *H. moquini* (based on filmed sequence) in a distraction-lure display in defence of young in response to our presence. (See text for details.)

ling them), the birds gave lower-intensity distraction-lure displays with less pronounced tilting of the body and sometimes did not flap their wings. Although both birds of a pair performed this display they never did it simultaneously, and the female did the bulk of the displaying.

Both sexes also performed "broken-wing" displays (Deane 1944) in which one or both wings were extended and trailed on the ground as the bird ran ahead of us. Another form of this display involved a bird which crouched in a crevice and irregularly flapped its partly folded wings. In contrast to the distraction-lure displays these "injury-feigning" lure displays (Williamson 1952) were given without vocalizations.

Birds incubating eggs did not give the elaborate distraction displays described above, but instead both sexes performed repeated bouts of "false brooding" (Makkink 1942) away from the nest-site. One pair with pipped eggs performed both false brooding and brief broken-wing displays.

Butterfly flights.—Adult *H. moquini* were often observed in "butterfly flights" (Huxley and Montague 1925) when flying across occupied territories in the breeding season. Following a prolonged bout of piping on the ground, one pair followed a departing intruder with an aerial chase. On the return flight the leading bird switched suddenly to butterfly flight with characteristically slow, exaggerated wing beats. Although most displays were given by one bird, up to three presumed pairs were observed

in group butterfly flights on Malgas Island in early January. In one example, the lead bird of a pair vocalized and performed butterfly flight above several territories, and in a return sweep both birds displayed. Another pair flew over and joined in with their butterfly flights, and eventually a third pair flew over and participated too. Since most birds on Malgas Island at this time of the year had young or eggs near hatching, these displaying birds were presumably failed breeders or newly formed pairs. On one occasion a bird ran slowly along the ground vocalizing with its wings raised high, and then took off and performed butterfly flight.

Fighting.—Fights occurred most often when birds were prospecting for mates and territories, or when piping displays failed to drive intruders from territories. Fighting usually consisted of charging with the bill thrust directly at the opponent's body. In some fights birds snatched at each other with partly opened bills, or grasped an opponent by the back of the neck and beat it with flapping wings while dragging it backwards. Fights were often followed by bobbing and displacement or "false feeding." Bouts of fighting were sometimes interrupted when one of the combatants adopted the "pseudo-sleeping" posture (Makkink 1942) by turning its head horizontally through 180° and hiding the bill in the scapulars. Unlike true sleeping, the eyes were kept open and focussed on the opponent when this posture was maintained. The pseudo-sleeping attitude was adopted frequently by both members of a pair when one of them returned to the territory after an absence. This posture may function to prevent aggressive interaction between members of a pair during a brief recognition period because we never saw attacks on birds adopting it.

VOCALIZATIONS

Piping.—Because piping displays usually involved several calling birds it was not always possible to identify which calls were made by particular individuals. However, we recorded a short segment of piping by one bird of a pair which was given in response to another bird which was emitting similar vocalizations during a distraction-lure display. The piping bird began with short "chip" calls which ascended in frequency, and then it switched to repeated units arranged in rising and falling couplets of lower and higher frequency calls (upper panel, Fig. 5). The bird progressively increased the loudness and frequency range of the first call in the couplets until they were subequal, and then it delivered a series of 11 long calls followed by a trill of "*pic*" calls called which ended the display (lower two panels, Fig. 5).

In longer displays, adult *H. moquini* cycled through this basic sequence of calls many times, though sometimes the beginning or concluding phrases of short notes were shortened considerably or even omitted. When

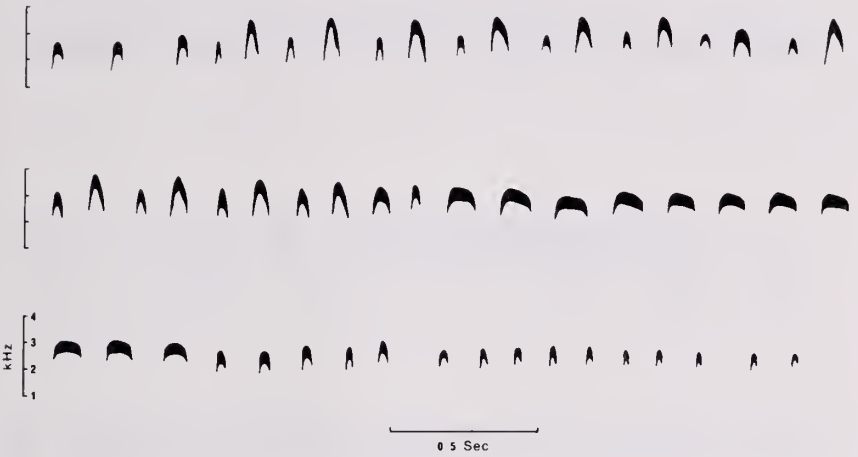

FIG. 5. Ground piping vocalizations given by one bird of a pair of *H. moquini*. Only the fundamental frequency of each call is shown.

both birds of a pair were piping together their sequences of calls were rarely similar. In several mutual displays we noted a tendency for the long calls of one bird to be followed by the long calls of its mate, but our samples are too small to test whether this resulted from synchronization or chance.

Distraction-lure vocalizations.—Three examples of the vocalizations accompanying the distraction-lure display are shown in Fig. 6. The major feature which distinguishes these vocalizations from those given in true piping is the rapid rate of repetition of calls. Two distinctive kinds of distraction-lure vocalizations were discernible in our recordings. In one kind the calls were short "*pics*" which usually graded into bi-peaked notes (Fig. 6A,B). These vocalizations are clearly composed of strings of alarm calls normally delivered at a much slower rate (cf. Fig. 7D and Fig. 8E–G). In the other kind of distraction-lure vocalization, which was most common, the calls are composed of regularly repeated couplets with alternating low and high frequency peaks (Fig. 6C), almost identical in arrangement to the second segment in piping (cf. Fig. 5).

The two kinds of distraction-lure vocalizations may reflect different motivational intensities of the displaying birds. The "alarm" kind of vocalizations in the two upper panels (Figs. 6A,B) were given when we were holding chicks in full view of their parents (high intensity), whereas the vocalizations in the lower panel (Fig. 6C) were given when we were standing near the rocks under which the chicks were hidden (lower in-

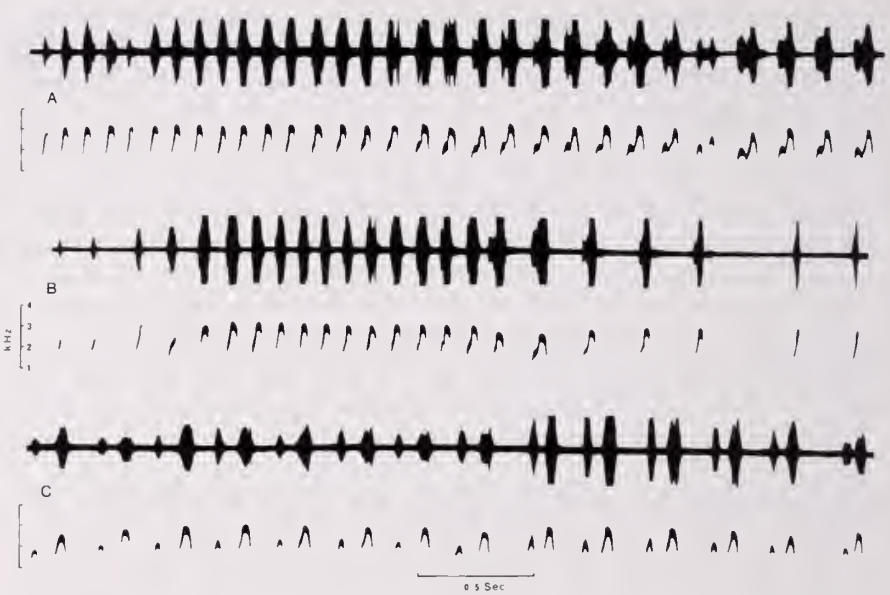

FIG. 6. Segments of distraction-lure display vocalizations of three different *H. moquini*. High intensity displays were given in response to chick distress calls (A,B), and low intensity forms were given when observers were near the hiding place of chicks (C). Only the fundamental frequency of each call is shown, with corresponding amplitude envelopes above.

tensity). Both sexes gave these vocalizations when attempting to lure us away from their chicks, although only one bird performed the display and vocalized at a particular time.

Alarm calls.—Hand-held chicks gave distress calls which varied with their age. Young chicks (ca 7–10 days old) gave spasmodic bursts of brief calls of similar frequency (Fig. 7A), but older chicks gave a variety of more complex calls involving rapid changes in frequency (Fig. 7B). Parents responded to these distress calls either with distraction piping or by emitting several different types of alarm calls. One bird gave trios of calls each of which began with a short chip followed by two long alarm calls (Fig. 7C), another gave complex two-part calls with different durations and frequency peaks (Fig. 7D), and other birds gave short *pic* calls which sometimes were emitted in pairs (Fig. 8E–G). Birds with eggs gave paired calls in which a short low frequency "chip" was followed by a longer and louder alarm call with a higher frequency peak (Fig. 8C–D). Both birds of a pair gave the same range of alarm calls and thus it was not possible to distinguish the sexes by their calls.

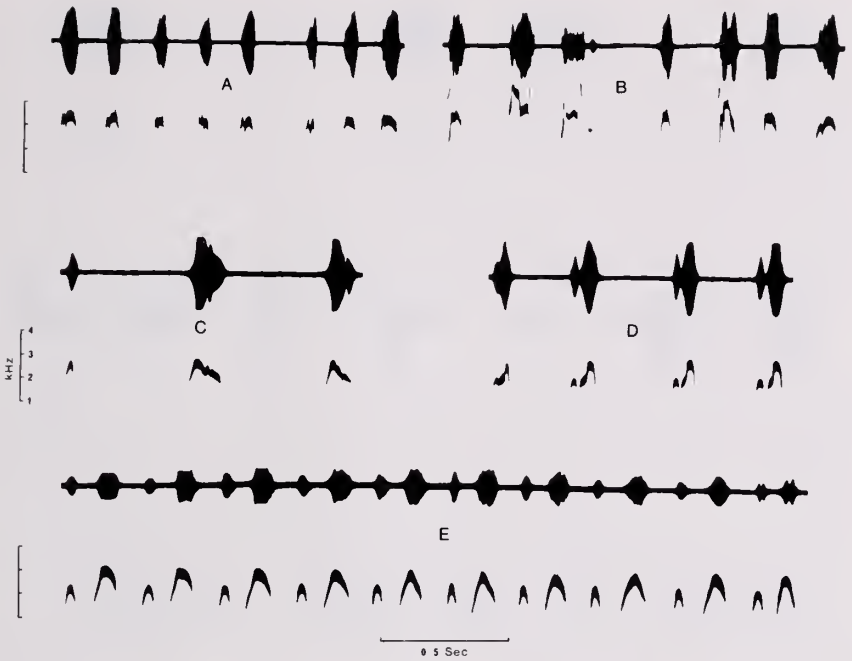

FIG. 7. Distress calls of chicks of *H. moquini* (A,B), alarm calls of adults given in response (C,D), and a segment of butterfly flight calls by an adult *H. moquini* (E). Only the fundamental frequency of each call is shown, with corresponding amplitude envelopes above.

Flight calls.—One adult *H. moquini* gave distinctive frequency and amplitude-modulated long calls when in flight (Fig. 8A). These calls are very similar to the *hueep* calls of New World species of oystercatchers (Miller and Baker 1980) which are given by pairs or single birds in flight, or by birds about to takeoff (Fig. 8B).

Birds performing butterfly flights often emitted vocalizations similar to those in the common form of the distraction-lure display. As in the latter, the calls are arranged in regularly repeated couplets of low and high frequency (Fig. 7E). The butterfly flight calls span a greater frequency range and are delivered at a slower tempo than their display-lure counterparts (cf. Fig. 6C). The slower tempo of the butterfly flight calls approximates the slow beat of the wings.

DISCUSSION

The behavioral and vocal repertoires of the African Black Oystercatcher are similar to those of other members of the Haematopodidae (except the

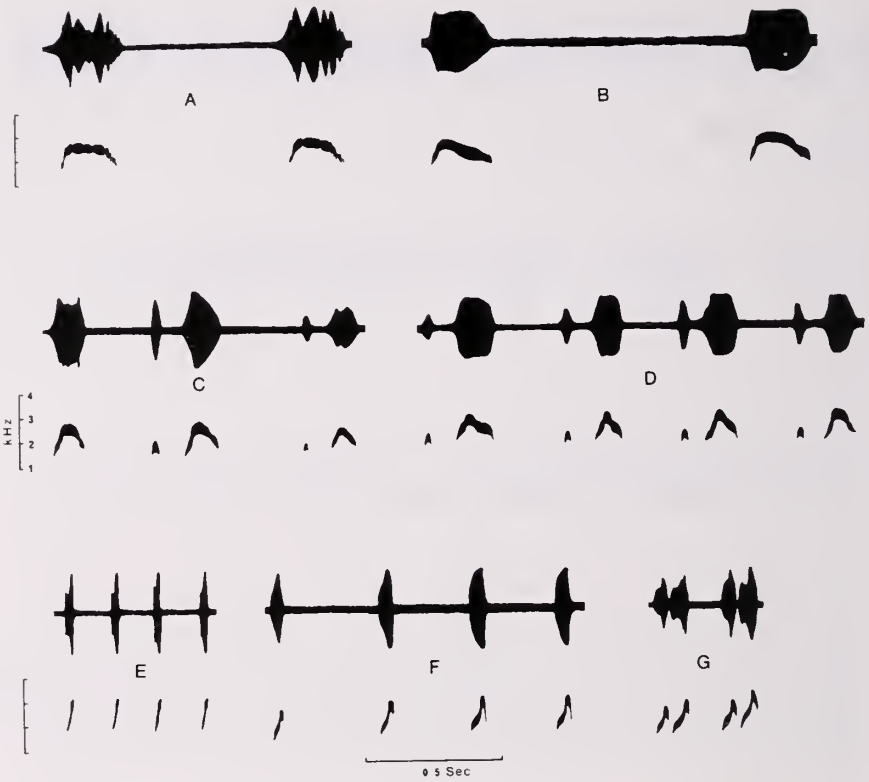

FIG. 8. *Hueep* flight calls (A,B), and alarm calls of adult *H. moquini* with eggs (C,D), and young (E,G). Only the fundamental frequency of each call is shown, with corresponding amplitude envelopes above.

aberrant Magellanic Oystercatcher [*H. leucopodus*]), and further support the contention that the Haematopodidae are an evolutionarily conservative group (Miller and Baker 1980). Despite this conservatism, *H. moquini* can be distinguished from other species of oystercatchers in specific aspects of its displays. The pre-copulatory display by the female appears to differ in *H. moquini* and the European Oystercatcher (*H. ostralegus*). In the latter the female assumes a passive posture while elevating the tail-end of the body (Makkink 1942), but in *H. moquini* the female appears only to crouch horizontally (Hall 1959, this study). Conversely, the "stealthy" approach of the male appears identical to that described for *H. ostralegus* (Huxley and Montague 1925, Makkink 1942).

Postures adopted by *H. moquini* during piping displays on the ground and in the air are very similar to those used by *H. ostralegus*. Both species

perform parallel runs in which the birds arch their necks downward and hold their bills vertically. All species of oystercatchers in the New World (forms with yellow irides and pale flesh-colored legs) raise the tail vertically (*H. leucopodus*) or obliquely (Blackish Oystercatcher [*H. ater*], American Oystercatcher [*H. palliatus*], and Black Oystercatcher [*H. bachmani*]) during the piping display (Kilham 1980, Miller and Baker 1980), but all Old World taxa (forms with scarlet irides and coral pink legs) hold their tails horizontally (Rittinghaus 1964; Glutz von Blotzheim et al. 1975, fig. 9; pers. obs.). Tail-raising is not an invariable component of piping in *H. palliatus* and *H. bachmani,* however, and is usually of short duration when it does occur.

The distraction displays of all species of oystercatchers need to be studied in more detail before substantive conclusions can be drawn about the systematic value of any variations. Nevertheless, it is already clear that the distraction displays of *H. moquini* closely resemble homologues in *H. ostralegus.* Both species distract potential predators with the same range of behaviors including false brooding, rodent runs, injury-feigning and distraction-lure displays. The form of the distraction-lure display in *H. moquini* is probably unique to the species. The homologous display in *H. ostralegus* apparently is given silently (Williamson 1943, 1950; but see Cramp et al. 1983 for a report of "unspecified piping calls" during this display) and does not involve the striking forward slanted posture or alternating erection and depression of the tail seen in *H. moquini.*

Butterfly flights in *H. moquini* are most often performed above territories in the breeding season when birds are prospecting for mates or breeding sites. Although the interpretation of this display in other species of oystercatchers has been problematical (see Cramp et al. 1983), most of the confusion seems to have stemmed from its use as a displacement activity, and this has obscured its principal function as an advertising or display flight. All species of oystercatchers perform butterfly flights (pers. obs.), and although the accompanying calls have only been studied spectrographically in *H. moquini,* the phonetic descriptions of these calls in *H. ostralegus* (Dircksen 1932, Cramp et al. 1983) strongly suggest their similarity.

Spectrographic analysis of the vocalizations of *H. moquini* has revealed that this species has a limited number of calls which have obvious counterparts in other species (see Miller and Baker 1980, and Cramp et al. 1983). In the New World *H. ater, H. palliatus,* and *H. leucopodus,* the piping vocalizations of each species are very similar to their respective alarm calls, suggesting that piping is a highly ritualized form of these calls (Miller and Baker 1980). In *H. moquini,* however, the introductory and

ending trills of piping resemble some alarm calls, and the couplets of low and high frequency notes in the second phrase are similar to the distraction-lure vocalizations.

The ground piping vocalizations of *H. moquini* are structurally distinct from those of *H. ater, H. palliatus,* and *H. leucopodus.* The latter species has unique narrow band vocalizations of almost constant frequency, whereas *H. palliatus* and *H. ater* have briefer wide band calls of varying frequencies (Miller and Baker 1980). Although the piping vocalizations of *H. moquini* are wide band and involve frequency shifts, their morphology is quite different from those of the New World species (cf. Fig. 5 this study and figs. 9–11 in Miller and Baker 1980). The piping calls of *H. moquini* are more similar to those of the Old World *H. ostralegus* than to the New World species (cf. call II in Cramp et al. 1983).

The vocalizations emitted during distraction-lure displays may be unique to *H. moquini,* although further sampling of calls of other species is required to substantiate this point. The close similarity of these calls to the second phrase in piping suggests that they have become ritualized in the distraction-lure display, and possibly in a slower and enhanced form in butterfly flight. Williamson (1952) argued that the distraction-lure display of *H. ostralegus* has evolved as a terrestrial modification of displacement butterfly flight. The close similarity of the vocalizations emitted during these displays in *H. moquini* lends support to this interpretation.

The alarm calls of all species of oystercatchers thus far studied are similar except in *H. leucopodus.* Most of the alarm calls of *H. moquini* are very similar to those of *H. ater, H. palliatus,* and *H. ostralegus* (cf. Figs. 7–8 this study, fig. 7 in Miller and Baker 1980, fig. 8A,B in Miller 1984, and calls V and VI in Cramp et al. 1983). In contrast to the New World species, however, both *H. moquini* and *H. ostralegus* have incorporated fewer of these types of alarm calls in their respective piping displays.

The *hueep* flight calls of *H. moquini* are almost identical to those of *H. ostralegus* (cf. Fig. 7A–B this study and calls I and II in Cramp et al. 1983). *Hueep* calls of *H. ater* and *H. palliatus* are longer and span smaller frequency ranges, thus distinguishing the New and Old World species.

While it is clear that further studies of oystercatchers are required to fully comprehend the evolution of display behavior in the Haematopodidae, nevertheless some useful conclusions can be drawn from this and earlier studies. The behavior and vocalizations of the African Black Oystercatcher strongly support its close affinity with the European Oystercatcher, but differences between them appear species-specific. The systematic value of similarties and differences in displays among oystercatcher species can best be assessed within a phylogenetic framework (Hennig

1966) which requires outgroup comparisons to determine whether character states are primitive or derived. Although Maclean (1972) pointed out problems of convergence and parallelism in display postures of Charadrii, detailed phylogenetic analysis not only can identify these problems but also can suggest which characters are useful in assessing relationships of taxa. Recent work using this approach on aerial displays of some species of Calidridinae has yielded very promising results (Miller 1983 a, b), confirming an earlier prediction that the systematic value of acoustic displays would be greatest in taxa using stereotyped sounds in long-distance communication and with little sound-learning (Mundinger 1979). These findings point up the need for broad comparative surveys of the behavior and vocalizations of shorebirds.

SUMMARY

The behavior and vocalizations of the African Black Oystercatcher (*Haematopus moquini*) were studied at Marcus and Malgas Islands in the southwestern Cape Province, South Africa. The behavioral and vocal repertoires of this species are broadly similar to other congeners, suggesting that the Haematopodidae are an evolutionarily conservative group. The African Black Oystercatcher has close affinity with the European Oystercatcher (*H. ostralegus*), based on the similarity of their piping postures, most distraction displays, alarm calls, and flight calls. These two species can be distinguished by differences in the pre-copulatory display of the female, the distraction-lure display, and possibly in piping vocalizations and butterfly flight calls. Assessment of the systematic value of these similarities and differences will depend on a future phylogenetic analysis with outgroup comparisons to determine character state polarities, and this in turn should encourage workers to attempt broad surveys of the behavior and vocalizations of shorebirds.

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FITZPATRICK INSTITUTE, UNIV. CAPE TOWN, RONDEBOSCH 7700, SOUTH AFRICA. (PRESENT ADDRESS AJB: DEPT. ORNITHOLOGY, ROYAL ONTARIO MUSEUM, 100 QUEEN'S PARK, TORONTO, ONTARIO, M5S 2C6 CANADA.) ACCEPTED 9 OCT. 1984.

CORRIGENDA 96:338 (1984)

P. 338, line 8 should read *Dendragapus canadensis*; lines 21–22 should read: . . . contradicts the text. Furthermore, I question the validity of placing the Spruce and Sharp-winged (*D. falcipennis*) grouse closer to the Blue Grouse. . . .

GENERAL NOTES

Wilson Bull., 96(4), 1984, pp. 672–680

Male Dickcissel behavior in primary and secondary habitats.—The Dickcissel (*Spiza americana*) is an early successional species nesting in weedy oldfields (Zimmerman, Auk 83:534–546, 1966; Auk 88:591–612, 1971; Harmeson, Auk 91:348–359, 1974). Fretwell and Calver (Acta Biotheoretica 19:37–44, 1969) suggested that Dickcissels have an ideal dominance distribution because habitat suitability, as indicated by female/male sex ratio, is higher in oldfield habitat where the density of individuals is higher, than in prairie where density is lower. Using nest survival rate and fledgling production, Zimmerman (Auk 99: 292–298, 1982) demonstrated the existence of the ideal dominance system for male Dickcissels, but found an ideal free distribution for females, since female fitness did not differ between habitats.

Females invest more energy per gamete than males, therefore females should be more selective of mates than males (Trivers, pp. 136–179 *in* Sexual Selection and the Descent of Man 1871–1971, E. C. Campbell, ed., Aldine Press, Chicago, Illinois, 1972). Females maximize their fitness by making optimum choices of male characteristics and territorial qualities, if these factors are assessable when they choose their mates (Searcy, Am. Nat. 114: 77–100, 1979a). The selective pressure of female choice on males of polygynous species results in the males evolving to choose and defend optimum habitat and/or to behave in a manner that would attract more females. Both territory quality and male quality may determine the reproductive fitness of the males (Wittenberger, Am. Nat. 110:779–799, 1976). Males defending territories of less than optimum quality may either compensate for this by emphasizing the displays in their repertoire that attract females, or may seek other territories of better quality.

In this paper I document the difference in habitat quality between primary oldfield habitat and secondary prairie habitat and its relationship with arrival times of males and females and female/male sex ratios. Primary habitat is defined as higher quality habitat where individual density is high, while secondary habitats have lower quality habitat and low individual density.

In addition, the behavior of male Dickcissels is analyzed to test predictions related to differences in habitat quality and selective pressures on males caused by female choice. I predict that Dickcissel males in primary habitat will spend more time defending their territories than those in secondary habitat, because there should be intense competition among males to obtain territories that will allow them to increase their fitness by sustaining higher levels of polygyny (Zimmerman 1982). Since female densities are higher in primary habitat, pressure to attract a mate is less than in secondary habitat. Therefore, I predict that secondary habitat males will spend more time in display behaviors that attract females, since territories in secondary habitats are generally of inferior quality and they are more dispersed within the habitat, while the pool of available females is small (Zimmerman 1966, 1971; Harmeson 1974). Schartz and Zimmerman (Condor 73:65–76, 1971) suggested that males on inferior territories spend more time away from their territories than those on superior territories because those males with inferior territories have a higher probability of locating territories more suitable than their own for attracting females than do males on superior territories. Therefore, I predict that secondary habitat males should spend more time in distant flight, a behavior in which a male temporarily leaves his territory, than primary habitat males; secondary habitat males might increase their fitness as a result of

such behavior if they could obtain better territories elsewhere. A male in an inferior territory would more likely switch territories if possible. Therefore, I predict that between-year site fidelity and within-year site tenacity should be lower in secondary habitat males than in primary habitat males.

Study sites and methods.—Four study sites were selected: an oldfield located approximately 15 km SW of Manhattan, in Riley Co., Kansas, on the eastern edge of the Fort Riley Military Reservation (Sec 30 T 10S R 7E) and three prairie sites about 11 km S of Manhattan in Riley and Geary counties within the boundary of the Konza Prairie Research Natural Area (KPRNA) (Secs 30 and 20 of T 11S R 8E). The study areas were marked with a 75-m square grid, corner positions being indicated by surveyor flags and/or 1-m wooden stakes. The study was conducted from the first week of May through the last week of August 1979.

The oldfield consisted of 30.4 ha of weedy forbs, grasses, and scattered woody species bounded on the north, west, and south by tree rows and on the east by a milo field. The area was dominated by sweet clover (*Melilotus officinalis* and *M. alba*), sunflower (*Helianthus* spp.), milkweed (*Asclepias* spp.), and lespedeza (*Lespedeza capitata*), with patches of daisy fleabane (*Erigeron strigosus*) and field bindweed (*Convolvulus arvensis*). Some patches of Canada wild rye (*Elymus canadensis*) were also present. Scattered woody species included small elms (*Ulmus americana*), American plum (*Prunus americana*), and smooth sumac (*Rhus glabra*).

The prairie sites consisted of 78.8 ha characterized by limestone shelves and dry creek beds. Big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), and Indian grass (*Sorghastrum nutans*) were the dominant grasses. Common forbs included lead plant (*Amorpha canescens*), New Jersey tea (*Ceanothus ovatus*), Baldwin ironweed (*Vernonia baldwinii*), and Atlantic wild indigo (*Baptisia leucophaea*).

Dickcissels were mist-netted and individually marked with colored leg bands. For all birds captured, flattened wing length was measured in mm as the distance from the bend of the wing to the tip of the longest primary (Baldwin et al., Sci. Publ. Cleveland Mus. Nat. Hist., No. 2, 1931). Bill length was the distance from the front of the nares to the tip of the bill. Bill depth was measured as the widest distance between the lower edge of the lower mandible to the upper edge of the upper mandible. The throat patch size was taken as the continuous length of the black throat patch, when the bird's neck was extended to a point just prior to spreading the neck feathers. Additional markings on the breast were also noted, but not measured. Mist-netting and visual identification were used to identify males banded the previous year.

Territory size was determined by flushing the males and recording their locations on grid maps (Wiens, Ornithol. Monogr. 8, 1969). Territorial boundaries were determined by observing interactions between neighbors as well as the location of perches used before and after flushing. Territory size was determined weekly by tracing the mapped territorial outlines with a compensating polar planimeter (K & E model 62–0000) and converting this reading to ha. Since Dickcissel territory size is affected by male density (Zimmerman 1971), all territories were adjusted to the same density for comparisons between males using the relationship $Y = 0.73627 - 0.1035X + 0.0005X^2$, where Y is the adjusted territory size and X is male density per 40 ha.

During June–August 1979, time budgets of 12 prairie and 21 oldfield males, randomly selected for this study, were recorded using the behaviors listed by Schartz and Zimmerman (1971): foraging, resting, singing, territorial defense, courtship, maintenance of the female, distant flight, and interspecific aggression. In addition, feeding young was also recorded. Observations were made using binoculars and a spotting scope. Behaviors were recorded at

TABLE 1

MEAN (± SE) FOR VEGETATION VARIABLES IN OLDFIELD (N = 36) AND PRAIRIE (N = 71)

		May	July	August
Vegetation vol.	Oldfield	1623 (±208.2)	3414 (±508.4)	5240 (±361.3)
	Prairie	621 (±45.9)	1926 (±106.4)	3133 (±110.0)
	t	6.22*	3.81*	7.04*
% grass	Oldfield	20.4 (±3.00)	16.1 (±2.61)	25.7 (±4.10)
	Prairie	26.7 (±1.68)	39.4 (±1.77)	50.3 (±1.71)
	t	1.97*	7.52*	6.52*
% forb	Oldfield	33.2 (±4.35)	38.6 (±3.84)	43.0 (±4.35)
	Prairie	12.4 (±1.27)	35.8 (±15.11)	23.5 (±1.64)
	t	5.84*	0.14	5.07*
Height	Oldfield	25.9 (±2.46)	53.6 (±5.94)	64.8 (±4.01)
	Prairie	14.7 (±0.51)	30.7 (±1.31)	41.7 (±1.35)
	t	5.76*	4.98*	6.74*

* $P < 0.05$.

10-sec intervals at the instant a beep was heard from a metronome timer (Wiens et al., Ecology 51:350–352, 1970). Behaviors were observed over 45-min periods, starting on the half hour from 06:30 until 20:30 CDT. There were 30 observation periods on the prairie and 75 in the oldfield.

Vegetation analysis was conducted in mid-May, early July and mid-August by using a modified point quarter technique (Greig-Smith, Quantitative Plant Ecology, 2nd ed., Butterworth, Washington, D.C., 1964). Randomly selected grid posts were used as sample sites. Ten randomly selected azimuths were used to obtain percent cover of forbs, grasses, and woody vegetation and the height of vegetation. Vegetation volume was calculated by multiplying percent vegetation cover by vegetation height.

Since data for particular behaviors were compiled as percent of total activity, they were transformed to arcsine (Zar, Biostatistical Analysis, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1974; Barr et al., SAS. User's Guide, SAS Institute Inc., Raleigh, North Carolina, 1979) for analysis of covariance in order to adjust the observations for variations in time, date, and temperature (see Schartz and Zimmerman 1971). The field season was divided into 2-week intervals for adjusted date and the day was divided into 2-h intervals for adjusted time.

The Spearman rank correlation was used for testing the association between male behaviors and the average number of females per week attracted to each territory (as determined by weekly censuses and nest counts). The relationship between the average number of females and the wing length, bill length, bill depth, and throat patch size of the territorial males was assessed using the Pearson product-moment correlation test. Differences in vegetation and the morphology of the males between oldfield and prairie habitats were analyzed by Student's *t*-test. The G-statistic was used to find differences between site fidelity and site tenacity for the males in the primary vs the secondary habitat.

Results.—Except for the coverage of forbs in July, there were significant differences between the vegetation in the oldfield and prairie sites throughout the breeding season (Table 1). Since the greater vegetation volume and the higher coverage by forbs in the oldfield is

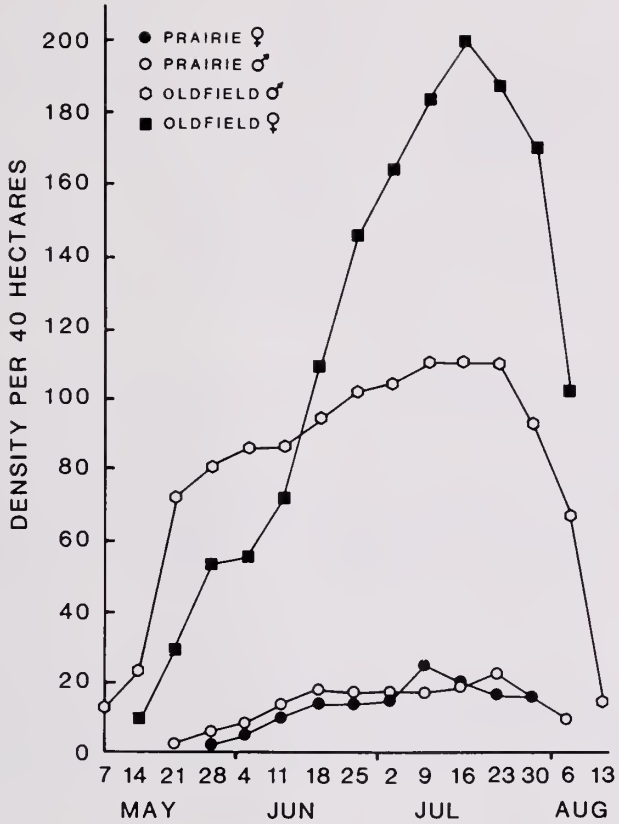

FIG. 1. The number of males and females per 40 ha in oldfield and prairie habitats for summer of 1979.

positively correlated with the incidence of polygyny (Zimmerman 1971), the oldfield habitat is preferred (primary habitat) more than the prairie (secondary habitat).

This difference in preference was reflected in the earlier arrival of Dickcissels in the oldfield (Fig. 1). Wittenberger (Condor 80:355–371, 1978) also found differential arrival for Bobolinks (*Dolichonyx oryzivorus*) in preferred vs other habitats, as did Carey and Nolan (Evolution 33:1180–1192, 1979) for Indigo Buntings (*Passerina cyanea*). Males arrived in the oldfield the first week of May and on the prairie during the third week of May. Females arrived during mid-May and late-May on the oldfield and prairie, respectively. Dickcissel density was also much higher on the oldfield than the prairie (Fig. 1). In the prairie, male density leveled off by the third week of June, whereas oldfield male density continued to increase until early July. Prairie female density remained constant from mid-June until late July, while oldfield female density sharply increased in early July before dropping off. Female/male sex ratio (Fig. 2) was higher in the oldfield than in the prairie at all times even with higher density in the oldfield, a pattern similar to that found by Fretwell and Calver (1969).

Oldfield males attracted a higher average number of females per week than prairie males

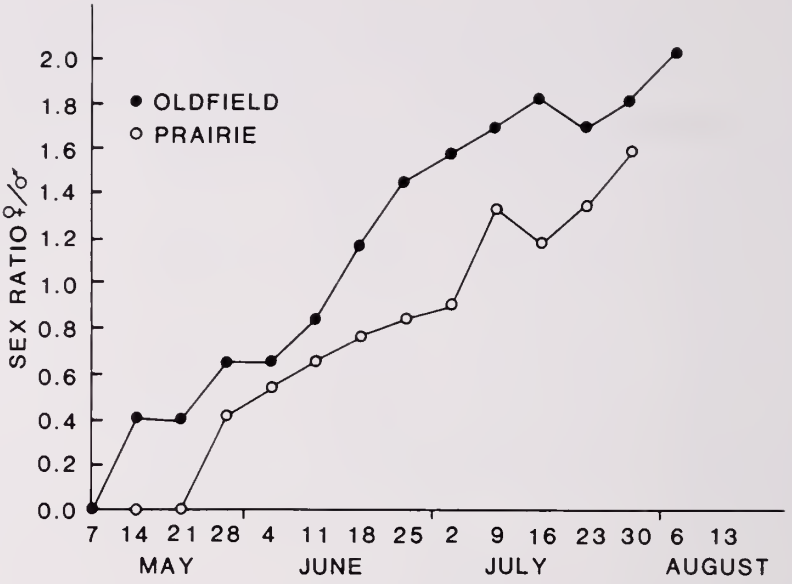

FIG. 2. The sex ratio (female/male) in oldfield and prairie habitats for summer of 1979.

($\bar{x}$ = 1.1, SE = ± 0.06, N = 140 and $\bar{x}$ = 0.8, SE = ± 0.05, N = 56, respectively; Student's t = 3.51, P = 0.006). The average number of females was positively correlated with adjusted territory size on both the prairie and the oldfield (r = 0.412, N = 56, P = 0.001 and r = 0.193, N = 140, P = 0.02, respectively), but adjusted territory size did differ between the two habitats with adjusted territories on the prairie significantly larger than in the oldfield ($\bar{x}$ = 0.50, SE = ± 0.036, N = 56, and $\bar{x}$ = 0.45, SE = ± 0.007, N = 140, respectively; Student's t = 1.98, P = 0.05).

Male morphology was not different between the two habitats with respect to wing length, bill length, bill depth, and throat patch size (Table 2). Since wing length is a measure of size (Connell et al., Auk 77:1–9, 1960), larger males did not occupy primary habitats to the exclusion of smaller males. The fact that bill length and depth were similar between habitats, suggests that the food types eaten in the two habitats may be similar.

Prairie males were present on their territories less than oldfield males, spending significantly more time in distant flight (Table 3). Prairie males also spent more time in courtship display, despite the fact that there were fewer females on the prairie, but less time in territorial defense, which is expected since male density was lower on the prairie. No other significant behavioral differences were observed between prairie and oldfield males. Male Dickcissels do not typically feed their young and the feeding observed in this study occurred rarely and then only in the oldfield late in the season when territorial drive had waned.

On the prairie, the only male behavior significantly correlated with average number of females attracted to a territory per week was resting (Table 4). This may reflect the fact that resting males sit on exposed perches and are conspicuous to females flying over the habitat. On the oldfield there was a negative correlation between time spent foraging by males and average number of females, which may be related to food density, which is higher on the oldfield than on the prairie. It may also reflect the fact that foraging males are less conspicuous

TABLE 2

MORPHOLOGICAL COMPARISONS OF DICKCISSEL MALES IN OLDFIELD AND PRAIRIE HABITATS

	Oldfield		Prairie			
	$\bar{x} \pm$ SE	N	$\bar{x} \pm$ SE	N	t	P
Wing length (mm)	82.6 ± 0.69	53	82.9 ± 1.25	8	0.36	NS
Bill length (mm)	10.43 ± 0.103	51	10.96 ± 0.109	8	1.69	NS
Bill depth (mm)	8.93 ± 0.003	42	8.97 ± 0.043	4	0.44	NS
Throat patch size (mm)	23.03 ± 2.236	50	19.58 ± 2.035	8	0.92	NS

* $P < 0.05$.

to females flying over and hence, fewer females are attracted to the territory. There was a positive correlation with throat patch size and average number of females only on the prairie (Table 4). In poorer habitats females may use male morphological qualities as selection cues in addition to behavioral ones.

There were no differences in site fidelity ($G = 0.156$, $df = 1$, $N = 28$, $P > 0.05$) or site tenacity ($G = 1.30$, $df = 1$, $N = 196$, $P > 0.05$) between resident males in the two habitats. Eleven of 18 (61.1%) oldfield males marked in 1979 returned in 1980, while 6 of 10 (60.0%) prairie males returned. Thirty-eight of 56 (67.9%) prairie males remained on their territories for more than two-thirds of the breeding season, while 81 of 140 (57.9%) oldfield males remained.

Discussion.—As predicted, primary habitat males did spend more time in territorial display than prairie males, which reflects the difference in male density between the two habitats. Since territorial display was not correlated with the average number of females attracted to the territory in either the oldfield or the prairie, this suggests that territorial display in Dickcissels functions in male-male competition for habitat rather than to attract females. When Dickcissel territory holders disappeared, replacement occurred within a couple of

TABLE 3

MALE DICKCISSEL BEHAVIORS[a] IN OLDFIELD AND PRAIRIE HABITATS

Behaviors	Oldfield %	Prairie %	F value (df = 1,102)
Distant flight	3.09	7.97	5.61*
Interspecific aggression	0.18	0.11	0.78
Resting	35.33	32.06	0.70
Singing	18.52	19.54	0.18
Territorial displays	1.42	0.68	2.90
Courtship	0.32	1.00	3.65
Foraging	35.35	34.44	0.21
Maintenance of females	5.73	4.20	0.08
Feeding young	0.02	0.00	0.42

[a] Adjusted for temperature, time, and date.
* $P < 0.05$.

TABLE 4

SIMPLE CORRELATION OF AVERAGE NUMBER OF FEMALES/WEEK ATTRACTED TO TERRITORIES AND MALE PHENOTYPE

	Oldfield		Prairie	
	N	r_s	N	r_s
Morphology				
Wing length	53	−0.039	8	−0.461
Bill length	51	−0.096	8	−0.172
Bill depth	42	−0.235	4	0.800
Throat patch size	50	−0.060	8	0.730*
Behavioral				
Distant flight	21	0.001	11	0.161
Interspecific aggression	21	0.060	11	0.031
Resting	21	0.308	11	0.596*
Singing	21	0.212	11	−0.018
Territorial defense	21	−0.241	11	−0.375
Courtship	21	−0.245	11	−0.282
Foraging	21	−0.477*	11	0.156
Maintenance of females	21	−0.101	11	−0.510

* $P < 0.05$.

days, which is another observation that supports the argument for intense competition for territories. By experimentally lowering male density, Orians (Ecol. Monogr. 31:285–312, 1961) demonstrated intense competition for territories in Red-winged Blackbirds (*Agelaius phoeniceus*). High intensity of territorial competition is also indicated by defense of suboptimal territories within primary habitat of Red-winged Blackbirds (Orians 1961), Dickcissels (Zimmerman 1966, 1971; Harmeson 1974; this study), and Bobolinks (Wittenberger 1978).

There was a negative correlation between foraging time and average number of females in the primary habitat, while in the secondary habitat there was a positive correlation with resting and average number of females; it appears therefore that male visibility may be important in attracting passing females even though the number of females a male attracts is not based on specific display behaviors (e.g., singing). Males on the prairie did not spend more time in behaviors that would attract more females. So this prediction was not met, yet prairie males compensated for their poorer territory quality and lower density of females by spending more time courting when the females were present. Because there were no differences in morphology between the males in the two habitats, these behavioral differences could be related to the demonstrated differences in habitat quality and associated with differences in female choice.

There are weak correlations with male behaviors and female choice in Red-winged Blackbirds (Weatherhead and Robertson, Wilson Bull. 89:583–592, 1977; Searcy, Auk 96:353–362, 1979b; Yasukawa, Ecology 62:922–929, 1981), as well as with Dickcissels (Finck, Ph.D. diss., Kansas State Univ., Manhattan, Kansas, 1983; this study). Verner (Evolution 18:252–261, 1964), Wittenberger (1976), Searcy (1979a), and Yasukawa (1981) suggested that it is

a combination of male quality and territory quality that forms the basis for female choice. Elsewhere (Finck 1983) I have shown that this is true in Dickcissels.

There was no greater site fidelity in oldfield males with better quality territories than prairie males with poor quality territories between years nor was there a difference in site tenacity between oldfield and prairie males. This may indicate that prairie males can not obtain better territories in more preferred habitats and instead maintain their fitness by increasing courtship and long distant flight. As the greater amount of distant flight in prairie males indicates, they still may spend more time looking for better territories during the breeding season on the chance that one is open.

The number of females on territories was positively correlated with adjusted territory size. However, Zimmerman (1966) and Harmeson (1974) found no correlation with unadjusted territory size and number of females in Dickcissels. Since territories in Dickcissels change with male density (Zimmerman 1971, Harmeson 1974, this study), unadjusted territory size is weighted by the density of males rather than being a true measure of territory size, which therefore masks the relationship between female numbers and territory size. The correlation of female numbers and adjusted territory size can not be accounted for by more available nest-sites alone, since adjusted territories are larger on the prairie, but prairie males have fewer females than oldfield males even though the number of females obtained by prairie males is still positively related to the adjusted territory size.

Dickcissel males must be able to assess the habitat quality of their territories, since prairie males spend more time off their territories than oldfield males and poor territory quality is correlated with increased distant flight (Schartz and Zimmerman 1971). They may do this by assessing density of males via the frequency of territorial song within a habitat or the intensity of encounters with territorial males that fly up to chase males intruding on distant flight.

Orians (1961) hypothesized that distant flight provided a means for increased foraging for male Red-winged Blackbirds. Yasukawa (Condor 81:258–264, 1979) showed that Red-winged Blackbird males who successfully occupied territories spent less time in distant flight than unsuccessful males. He attributed this to increased foraging off the territories by unsuccessful males because distant flight and foraging equaled the foraging on territories by successful males. However, it is possible that these unsuccessful males obtained territories elsewhere. In this study there was no difference between the amount of time spent foraging by the oldfield males and that spent by the prairie males. The prairie males spent more time (42.4%) in the combination of distant flight and foraging than oldfield males did in foraging (35.5%). This suggests that other factors may influence distant flight in Dickcissels.

Schartz and Zimmerman (1971), Martin (Am. Zool. 14:109–119, 1974), and Nolan (Ornithol. Monogr. 26, 1978) hypothesized that distant flight functioned as a mechanism for exploring potential territories. This could be very important for an early successional species such as the Dickcissel. Schartz and Zimmerman (1971) suggested that during distant flight males evaluated population densities. In support of this idea they found a correlation with poor quality territories, as measured by the number of females on territories, and increased distant flight. In this study I have demonstrated that individuals in poor habitat are in distant flight more than individuals in good habitat. Zimmerman (1982) has shown that male fitness is higher in habitats with higher male density.

A male Dickcissel that leaves his territory may find a better site and/or a potential mate. He may lead that mate back to his territory, copulate with her at the new site or switch territories. Many male passerines have been seen singing off of their territories and copulating with females (Ford, pp. 329–356 *in* Current Ornithology, Vol. 1, R. F. Johnston, ed., 1983). I have seen three instances of male Dickcissels singing off their territories and a non-resident

male displaying towards a receptive female in another male's territory. Also, territory switches occur during the season. There was also an instance in which a male Dickcissel left his territory for 3 weeks and returned with a female. Some female Red-winged Blackbirds on territories of vasectomized males have still been known to produce young (Bray et al., Wilson Bull. 87:195–197, 1975). Keller (M.S. thesis, Univ. North Dakota, Grand Forks, North Dakota, 1979) suggests that in Chipping Sparrows (*Spizella passerina*) an alternative strategy to holding a good territory could be to sneak copulations, provided that the male does not spend much time off his territory or his female may be inseminated by other wandering males. The role of distant flight and switching territories needs further investigation. In birds such as the Dickcissel, both strategies could increase fitness.

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Passage rate, energetics, and utilization efficiency of the Cedar Waxwing.—The Cedar Waxwing (*Bombycilla cedrorum*) is noted for its intensive foraging on fleshy fruits (Nice, Condor 43:58–64, 1941; Tyler, U.S. Natl. Mus. Bull. 197:79–102, 1950). Flocks of Cedar Waxwings have been reported to deplete entire fruit crops of red cedar (*Juniperus virginiana*) over a period of 2 days (Parker, Ph.D. diss., Duke Univ., Durham, North Carolina, 1949). In summer the diet of the Cedar Waxwing is composed largely of insects and fleshy fruits and in winter their food consists almost exclusively of fruits (Beal, pp. 197–200 *in* Ann. Rept. Dept. Agric. 1892, and Farmer's Bull. 54:38–39, 1904; Nice 1941; Tyler 1950; Martin et al., American Wildlife and Plants, Dover Publ. Inc., New York, New York, 1951). The Cedar Waxwing is therefore considered a major frugivore (Thompson and Willson, Evolution 33:973–982, 1979; Stiles, Am. Nat. 116:670–688, 1980). However, the extent to which the Cedar Waxwing can subsist on fruits alone has not been investigated.

Nutritional studies of fruit-eating passerines in Europe have shown that all species except the Bohemian Waxwing (*Bombycilla garrulus*) rapidly lose weight and die in captivity if supplied only with fruits (Berthold, J. Orn. 117:145–209, 1976a; Experientia 32:1445, 1976b; Ardea 64:140–154, 1976c; J. Orn. 118:202–203, 1977). Therefore, Berthold (1976b) considered the Bohemian Waxwing a fruit specialist, as opposed to an opportunistic frugivore. A similar adaptation to a frugivorous diet may be expected from the Cedar Waxwing, since this bird closely resembles the Bohemian Waxwing in its food habits (Bent, U.S. Natl. Mus. Bull. 197:62–79, 1950; Tyler 1950).

In this study we assessed the energy requirements, the rate and efficiency of digestion, and the ability of captive Cedar Waxwings to survive on a diet of fleshy fruits during autumn. The investigations were part of a larger research project on the role of Cedar Waxwings as seed dispersers of red cedar, a common woody tree species in eastern North America.

Materials and methods.—Cedar Waxwings were caught on the campus of the Virginia Polytechnic Institute and State University, Blacksburg, Montgomery Co., Virginia, in the autumn of 1980 (N = 5) and 1981 (N = 6). Each bird was placed in a separate, wire mesh (0.5 cm) cage, measuring 80 × 60 × 45 cm. The Cedar Waxwings were kept in an unheated room allowing free circulation with outside air ($\bar{x}$ = 12°C during the day; $\bar{x}$ = 5°C at night), on an 11-h light, 13-h dark cycle, simulating the natural photoperiod. The birds were supplied ad libidum with water and a mixture of fruits, including those of cork-tree (*Phellodendron sachalinense*), cherry (*Prunus* sp.), mountain ash (*Sorbus americana*), viburnum (*Viburnum* sp.), privet (*Ligustrum vulgare*), multiflora rose (*Rosa multiflora*), honeysuckle (*Lonicera morowii*), flowering dogwood (*Cornus florida*), and red cedar (*Juniperus virginiana*). All foodstuff was collected locally and stored in a refrigerator.

Observations on feeding and defecation rates were made on four Cedar Waxwings provided with red cedar cones in the autumn of 1980; the observations were repeated with four different birds in 1981. In 1981, similar observations were made on two Cedar Waxwings supplied with flowering dogwood fruits. All food was removed from the cages on the evening before each observation period. The next morning, 14–16 h later, the birds were weighed and provided with fruits. Direct observations, made at a distance of 1–2 m from the birds, included time of feeding, number of fruits ingested per feeding bout, and time of defecation. The birds were supplied with a mixture of fruits upon termination of each experiment. The passage rate of red cedar and dogwood seeds in the alimentary tract of Cedar Waxwings was estimated by applying 1–2 cc of an inert marker (ferric-oxide in solution) directly into the bird's esophagus immediately before the start of an experiment. The passage rate represented the time between ingestion of the first fruit at the start of the experiment and the appearance of the first colored dropping.

The energy requirements of the Cedar Waxwing were determined using five birds caught in 1980. An estimation of the existence metabolism can be obtained, if captive birds sustain their weight, as shown by Kendeigh (Wilson Bull. 81:441–449, 1969; Condor 72:60–65, 1970; Am. Nat 106:79–88, 1972). The existence metabolism is a reasonable approximation of the energy requirements of a bird under free living conditions (Kendeigh 1969, 1970). The five Cedar Waxwings were starved for 16 h prior to the start of the experiment. Their daily energy requirements were determined over a period of 6 days. The birds were weighed each morning and supplied with known amounts of mountain ash, cork-tree and *Viburnum* sp. fruits in excess of the bird's daily use as established prior to the start of the experiment. The first 2 days of the experiment were excluded from the analysis to allow the birds to adjust to their diet (Sibbald, pp. 38–43 *in* Standardization of Analytical Methodology for Feeds, W. J. Pigden et al., eds., Workshop Proc., 12–14 March 1979, Ottawa, Ontario, 1980). Each morning, all fecal material and remaining fruits were collected from the cages and weighed. Fecal material was stored in plastic bags in a refrigerator. Percent dry matter of fecal material and fruits was determined according to procedures described by the Association of Official Agricultural Chemists (Methods of Analysis, Washington, D.C., 1975). The fecal material and samples of the foodstuff (including seeds) were ground in a Wiley mill after drying, sieved (mesh size 600 μm), and pelleted for caloric determination (kcal/g dry weight) in a Parr adiabatic oxygen bomb calorimeter. The metabolized energy was determined by subtracting the caloric fecal energy (kcal/g dry weight) from the gross energy intake. The average energy metabolized over 4 days provided an estimate for the existence metabolism of the Cedar Waxwing (Kendeigh 1972). Utilization efficiencies of Cedar Waxwings

TABLE 1

METABOLIZED ENERGY (ME IN KCAL/DAY), UTILIZATION EFFICIENCY (%), AND BODY WEIGHT (G) OF CEDAR WAXWINGS IN CAPTIVITY CALCULATED OVER A 4-DAY PERIOD[a] IN NOVEMBER 1980

ME		Utilization efficiency (%)	Bird weight (g)	
Bird	(kcal/day)		$\bar{x}$ ± SD	N
1	30.5	53.1	24.8 ± 0.5	4
2	17.8	26.6	35.5 ± 0.7	4
3	25.3	36.1	30.3 ± 0.4	4
4	23.7	35.2	28.2 ± 0.9	4
5	21.2	31.3	31.5 ± 0.5	4
$\bar{x}$	23.7	36.5	30.1 —	—
SD	4.8	10.0	3.6 —	—
N	5	5	20 —	—

[a] Referred to as existence metabolism (Kendeigh 1969). Birds were fed with a mixture of fruits (*Sorbus* sp., *Viburnum* sp., *Ligustrum* sp., and *Phellodendron sachalinense*).

fed on a diet of mixed fruits were calculated according to the formula $(E_i - E_e)/E_i$, where E_i = ingested energy content of the food (kcal) and E_e = fecal energy (kcal) (Walsberg, Condor 77:169–174, 1975). All calculations and tests were made using the Statistical Analysis System (SAS) (Helwig and Council, The SAS User's Guide, 1979 ed., The SAS Inst. Inc., Cary, North Carolina, 1979). Means are followed by standard deviations.

Feeding, defecation, and passage rates.—The total observation time of Cedar Waxwings provided with red cedar cones or dogwood fruits amounted to 44.32 h and 10.12 h, respectively. Cedar Waxwings fed on red cedar cones approximately every 5 min (4.93 ± 4.85 min, N = 485) and consumed on the average 4.4 ± 3.5 (N = 522) red cedar cones per feeding bout. The extrapolated feeding rate is 53 cedar cones per hour. Cedar Waxwings provided with dogwood fruits foraged at shorter intervals, 3.10 ± 3.78 min (N = 323) ($t = -5.97$, df = 786, $P < 0.0001$), but only consumed one fruit per feeding bout, which resulted in a feeding rate of 19 dogwood fruits per h. The passage rate of red cedar cones was significantly shorter ($t = 6.05$, df = 54, $P < 0.001$) than the passage rate of dogwood fruits (11.67 ± 4.23 min, N = 40 and 22.92 ± 6.92 min, N = 16, respectively). The mean defecation rate, however, was longer ($t = -5.87$, df = 1080, $P < 0.0001$) for Cedar Waxwings feeding on red cedar cones than those feeding on dogwood fruits (2.82 ± 3.73 min, N = 705 and 2.08 ± 1.42 min, N = 378, respectively). Defecation rates were not different between birds administered the marker solution and those not ($t = 1.37$, df = 696, $P = 0.17$, for red cedar cones; $t = -0.77$, df = 376, $P = 0.43$, for dogwood fruits).

Existence metabolism.—Under laboratory conditions five Cedar Waxwings used, on average, 23.7 ± 4.8 kcal/day; the utilization efficiency averaged 36.5 ± 10.0% (Table 1). The body weights of the birds remained stable during the 4 days of the experiment, as indicated by a standard deviation of less than 1 g per bird (Table 1). In 1981, the six Cedar Waxwings were kept in captivity for up to 27 days. During this period their body weights fluctuated within narrow limits, up to 4.8% of the mean body weight ($\bar{x}$ = 31.2 ± 1.5 g, N = 162). The Cedar Waxwings did not show a change in body weight over time: no significant linear relationships ($0.01 < F < 0.68$, df = 1 and 24, $0.4 < P < 0.9$) could be established between the differences in weight of individual birds on subsequent days in captivity.

Discussion.—Cedar Waxwings have been reported to digest fleshy fruits rapidly. Nice (1941) fed cherries and blueberries (*Vaccinium* sp.) to a juvenile Cedar Waxwing and reported a passage rate varying from 16–40 min. A 20-min passage rate was measured by Maynard (Bull. Northeastern Bird Banding Assoc. 4:73–76, 1928) for cherry stones, and Stevenson (Wilson Bull. 65:155–167, 1933) estimated a passage rate of 100 min for raspberries (*Rubus* sp.) fed to two juvenile Cedar Waxwings. However, Maynard (1928) and Nice (1941) did not starve their birds prior to the start of the experiments, and Stevenson (1933) did so only for 2 h. Passage rates have been investigated to a greater extent with the Bohemian Waxwing. Cvitanic (Larus 12:51–53, 1958) fed *Ligustrum* sp. fruits to a Bohemian Waxwing, which was starved for 24 h, and observed seeds in feces after 10 min. In another experiment with *Pyracantha coccinea* fruits, a mean passage rate of 11 min was recorded, but on this occasion the bird was not starved (Cvitanic 1958). Feeding trials with *Symphoricarpos albus, Viscum album, Viburnum opulus,* and *Sorbus aucuparia* conducted by Borowski (Przeglad Zoologiczny 10:62–64, 1966) with a Bohemian Waxwing, showed that 50% of the ingested seeds were voided after 13.5–27.5 min. Digestion of marked mistletoe berries (*Phorodendron californicum*) by the Phainopepla (*Phainopepla nitens*), a fruit specialist similar in weight to the Cedar Waxwing, took 29 min (Walsberg 1975). The above mentioned estimates of passage rates for the Cedar Waxwing, Bohemian Waxwing, and Phainopepla are of the same order of magnitude as those found in this study, in spite of considerable differences in experimental conditions (e.g., foodstuff and starvation time). Thus, the passage rate observed in these frugivores is relatively short.

Differences in passage rates of fruits found for our Cedar Waxwings (i.e., 23 min for dogwood fruits and 12 min for red cedar cones) may be partly attributed to differences in digestibility of the fleshy fruits with which the experiments were conducted. Dogwood fruits are heavier than cedar cones (0.14 g vs 0.01 g; Halls, Southern Fruit-producing Woody Plants Used by Wildlife, U.S. Dept. Agric. For. Serv. Gen. Tech. Rept. SO-16, South. For. Expt. Stn., New Orleans, Louisiana, 1977) and the fruit pulp also contains a higher percent crude fat (16.7 vs 6.8%; Halls 1977).

The metabolized energy (ME = 23.7 ± 6.1 kcal per day) found for Cedar Waxwings in captivity is within the range of the metabolized energy estimated using Pimm's (Condor 78: 121–124, 1976) functional relationship between existence metabolism and body weight, ambient temperature and photoperiod (mean body weight of five Cedar Waxwings during the experiment = 30.1 g (N = 20), mean temperature = 8°C, photoperiod = 11 h; ME = 20.5 kcal/day).

The feces of Cedar Waxwings feeding on fleshy fruits were pulpy and contained many undigested fruit skins, perhaps a reflection of their low utilization efficiency (36.5%). The low utilization efficiency is similar to that reported for two other fruit feeders (Phainopepla, 49%, Walsberg 1975; Townsend's Solitaire [*Myadestes townsendi*], 37.6%, Salomonson and Balda, Condor 79:148–161, 1977). These data support the generalization that frugivores have lower utilization efficiencies than granivores (70%–90%, Kendeigh et al., pp. 127–204 *in* Granivorous Birds in Ecosystems, J. Pinowski and S. C. Kendeigh, eds., Int. Biol. Prog. 12, Cambridge Univ. Press, Cambridge, Massachusetts, 1977).

During 27 days of captivity the Cedar Waxwings were able to subsist on a fruit diet, suggesting that they are fruit specialists sensu Berthold (1976b). Similar experiments may be conducted with other frugivores to develop a relative scale of frugivory among birds now rather arbitrarily classified as "frugivores" or "major frugivores" (Stiles 1980).

Cedar Waxwings are reported to feed extensively on red cedar cones in winter in southeastern North America (Tyler 1950; Martin et al. 1951). Red cedar cones contain 56.4 ± 13.1 cal/cone (N = 36), excluding the seeds (Holtuijzen, Ph.D. diss., VPI & SU, Blacksburg, Virginia, 1983). These data suggest that Cedar Waxwings would have to consume about

twice as many cones as did our captives for maintenance during inactivity (1159 cones/day vs 583 cones/11-h day in this study). Clearly, the numbers of red cedar cones required by free-living birds would be much greater, but it is not known whether they could actually digest red cedar cones rapidly enough to cover their energy requirements.

The Cedar Waxwing subsists on a large variety of woody plant fruits for most of its nutrition during the fall and winter months. Since the Cedar Waxwing has a low utilization efficiency, it probably consumes large quantities of various fruits. This also implies that large quantities of seeds may pass through the digestive tract, perhaps in a viable condition as was found for red cedar seeds (Holthuijzen and Sharik, Virginia J. Sci. 34:123, 1983). Thus, the Cedar Waxwing may be a major disperser of fruit-bearing plants in eastern North America.

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Short-term changes in bird communities after clearcutting in western North Carolina.—Logging practices have been under increasing scrutiny because of their effects on biotic communities. Songbird populations as integral components of such communities are subject to disturbance by logging. Two goals involving management of songbird populations have surfaced in the literature: to maximize bird species diversity and to protect habitat of endangered and threatened species (Lennartz and Bjugstad, pp. 328–333 *in* USDA For. Serv. Gen. Tech. Rept. WO–1, 1975). The primary objective of this study was to examine effects of clearcutting on the breeding-bird community during the early years of vegetation regrowth, when changes in the avifauna are likely to be greatest.

The relationship of avian communities to timber harvesting in eastern forests has been the subject of several studies. Clearcutting of hardwood forests usually has resulted in an increase in bird species diversity (Ambrose, Ph.D. diss., Univ. Tennessee, Knoxville, Tennessee, 1975; Conner and Adkisson, J. For. 73:781–785, 1975; Nyland et al., Tappi 60:58–61, 1977), whereas, heavy cutting of a pine-oak woodland led to decreased diversity (Conner et al., Wilson Bull. 91:301–316, 1979). Changes in guild structure or other community attributes were not analyzed. Thus, a second objective of the present research was to examine changes in the bird community other than species diversity.

Study areas and methods.—The study was conducted in the Highlands Ranger District, Nantahala National Forest, North Carolina. The Highlands Plateau lies adjacent to the Blue Ridge Escarpment and contains an unusually diverse biota in comparison with the remainder of the southern Appalachians (Oosting and Billings, Am. Midl. Nat. 22:333–350, 1939). The Highlands Biological Station has provided a base from which the distribution and ecology of the avifauna have been studied for many years (see Johnston, J. Elisha Mitchell Sci. Soc. 80:29–38, 1964; and Holt, Wilson Bull. 86:397–406, 1974, for summaries). With an average elevation of 1200 m, the plateau's forests attract typically northern species such as Golden-crowned Kinglets (*Regulus satrapa*), Rose-breasted Grosbeaks, and Dark-eyed

TABLE 1
TERRITORIAL MALES PER KM²

Guild[a]	Bird species	Ellicott Rock		Rich Mt.		Brush Creek		Horse Cove	
		1975[b1]	1976[2]	1975[2]	1976[3]	1975[3]	1976[4]	1975[4]	1976[5]
2OH	Ruby-throated Hummingbird (*Archilochus colubris*)	—	12	7	7	—	—	—	—
1IH	Carolina Chickadee (*Parus carolinensis*)	—	12	—	7	—	—	—	6
1IH	Tufted Titmouse (*P. bicolor*)	—	—	—	—	—	—	—	3
3IL	Winter Wren (*Troglodytes troglodytes*)	—	—	—	—	—	6	—	—
2IL	Carolina Wren (*Thryothorus ludovicianus*)	25	31	7	7	12	—	16	25
2IL	Gray Catbird (*Dumetella carolinensis*)	—	—	14	14	12	12	12	6
2OL	Brown Thrasher (*Toxostoma rufum*)	—	—	—	—	—	—	6	12
2IL	White-eyed Vireo (*Vireo griseus*)	—	—	—	—	—	—	16	12
3IL	Golden-winged Warbler (*Vermivora chrysoptera*)	—	—	—	7	—	6	—	—
2IH	Black-throated Blue Warbler (*Dendroica caerulescens*)	—	6	—	—	—	—	—	—
2IH	Chestnut-sided Warbler (*D. pensylvanica*)	—	25	28	82	25	69	31	38
2IL	Yellow-breasted Chat (*Icteria virens*)	—	—	—	—	—	—	3	6
2IL	Hooded Warbler (*Wilsonia citrina*)	—	—	—	—	—	—	—	12
3IH	Canada Warbler (*W. canadensis*)	—	—	—	—	6	9	—	—
2OL	Cardinal (*Cardinalis cardinalis*)	—	—	—	—	3	—	6	6
2IL	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	—	—	7	14	3	—	—	—
2OH	Indigo Bunting (*Passerina cyanea*)	25	50	21	21	6	6	19	12
3OL	Rufous-sided Towhee (*Pipilo erythrophthalmus*)	50	75	28	39	25	38	19	31
3OL	Dark-eyed Junco (*Junco hyemalis*)	—	—	—	7	—	—	—	—
Total individuals		100	211	112	205	92	146	128	169
Total species		3	7	7	10	8	7	9	12

[a] Guild designations: nest located (1) in cavities, (2) in thickets, or (3) on ground; feeding (O) omnivorous or (I) insectivorous; foraging height (L) low or (H) high.
[b] Superscript indicates number of breeding seasons since logging.

FIG. 1. Values of the Shannon diversity index, H′, plotted against stand age. Open circles and dashed line indicate Highlands sites; closed circles and solid line are data from southwestern Virginia (Conner and Adkisson 1975). P = pole stand, M = mature forest.

Juncos, but lack many species found at lower elevations, including Eastern Bluebirds (*Sialia sialis*), and Red-bellied Woodpeckers (*Melanerpes carolinus*). (Scientific names not given in text are in Table 1.)

Within this escarpment four sites were selected and censused throughout two consecutive breeding seasons. The sites ranged in age from one to four seasons after logging in 1975 and two to four seasons in 1976. Size, elevation, and site index (average height of major hardwoods after 50 years of growth) were: Ellicott Rock, 8 ha, 880 m elev., 71; Rich Mountain, 14 ha, 1200 m elev., 73; Brush Creek, 16 ha, 1200 m elev., 91; Horse Cove, 16 ha, 950 m elev. 91. All exposures were east or southeast. Each area had been clearcut during the winter without site preparation and all marketable timber removed. Importance values (relative frequency plus relative density) before logging for white oak (*Quercus alba*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), and white pine (*Pinus strobus*) were: Ellicott Rock, 31, 22, 10, 31; Rich Mt., 35, 24, 26, 33; Brush Creek, 11, 23, 45, 0; Horse Cove, 28, 44, 12, 45. After logging oak and hickory (*Carya* spp.) sprouts were prominent but subordinate to sprouts of red maple (*Acer rubrum*) at all sites. Seedlings of tuliptree (*Liriodendron tulipifera*) increased with time since logging; by the fifth season they surpassed red maple in importance value. There was little regeneration of white pine. Vegetation on the first-year site was very sparse in spring but nearly covered the ground by autumn. Plant height averaged 1 m at the first-year site and 3–4 m at the fifth-year site. Numbers of stems per ha after logging for all tree species were: Ellicott Rock 5200; Rich Mt. 12,700; Brush Creek 10,500; Horse Cove 7400. A more complete description of the sites and their vegetation is available in Horn (Castanea 45:88–96, 1980).

Breeding bird censuses were made between 11 May and 5 July by the spot-map method (Van Velzen, Am. Birds 26:1007–1010, 1972). Each area was mapped, with flagged stakes placed every 50 m to facilitate plotting of bird observations on the map. Following the

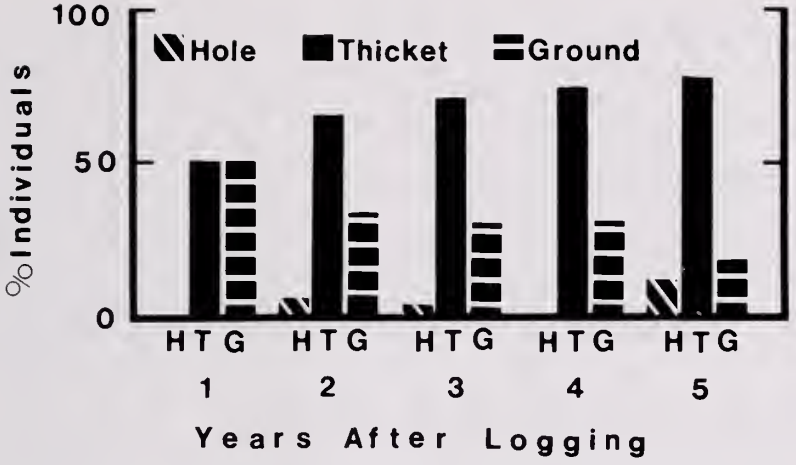

FIG. 2. Percentage of individuals in various nest guilds at the Highlands clearcuts. H = cavity or hole guild; T = thicket guild; G = ground guild.

recommendations of Best (Auk 92:452–460, 1972), I included all bird encounters and registered males singing simultaneously. Because of concurrent vegetation sampling only four formal censuses per site were made in 1975, although much non-census time was spent at each area. Ten trips per site were made in 1976. All visits took place between dawn and 09:00. In analyzing data, at least three song encounters (or two song encounters with simultaneous registration and supportive sightings) were used to determine a territory. Census results were relativized to 100 ha (1 km^2).

The limited number of formal census trips in 1975 probably resulted in underestimated numbers on all but the first-year site. The denuded vegetation of that site neither attenuated songs nor hindered complete, rapid coverage, allowing an accurate census from a few trips. Because of this difference in censusing between years, the 1975 data from all but the first-year site were excluded from the analysis.

For comparison with other work it was necessary to compute the Shannon diversity index, H′ (Pielou, An Introduction to Mathematical Ecology, John Wiley and Sons, New York, New York, 1969). In addition, changes in nest and food guilds were examined. Guilds for each species were determined from data in Bent (U.S. Natl. Mus. Bull. 176, 1940; 191, 1946; 195, 1948; 197, 1950; 203, 1953; 237, 1968) and Willson (Ecology 55:1017–1029, 1974). Nest locations were separated into: (1) cavities, (2) ground, and (3) thickets below 3 m in height. Feeding categories were: insectivores (I) vs omnivores (O) and low foragers (L) vs high foragers (H). The number of individuals in each guild was determined for every area, and the resultant table analyzed for independence of rows (guilds) and columns (years since logging) using Chi-square analysis (Steel and Torrie, Principles and Procedures of Statistics, McGraw-Hill, New York, New York, 1960:366).

Results and discussion.—Four species were found at nearly all sites both years, and can be considered characteristic of young clearcuts in this area: Carolina Wren, Rufous-sided Towhee, Indigo Bunting, and the dominant Chestnut-sided Warbler (Table 1). At the two youngest sites, forest species foraged only along the periphery. In older clearcuts they spent

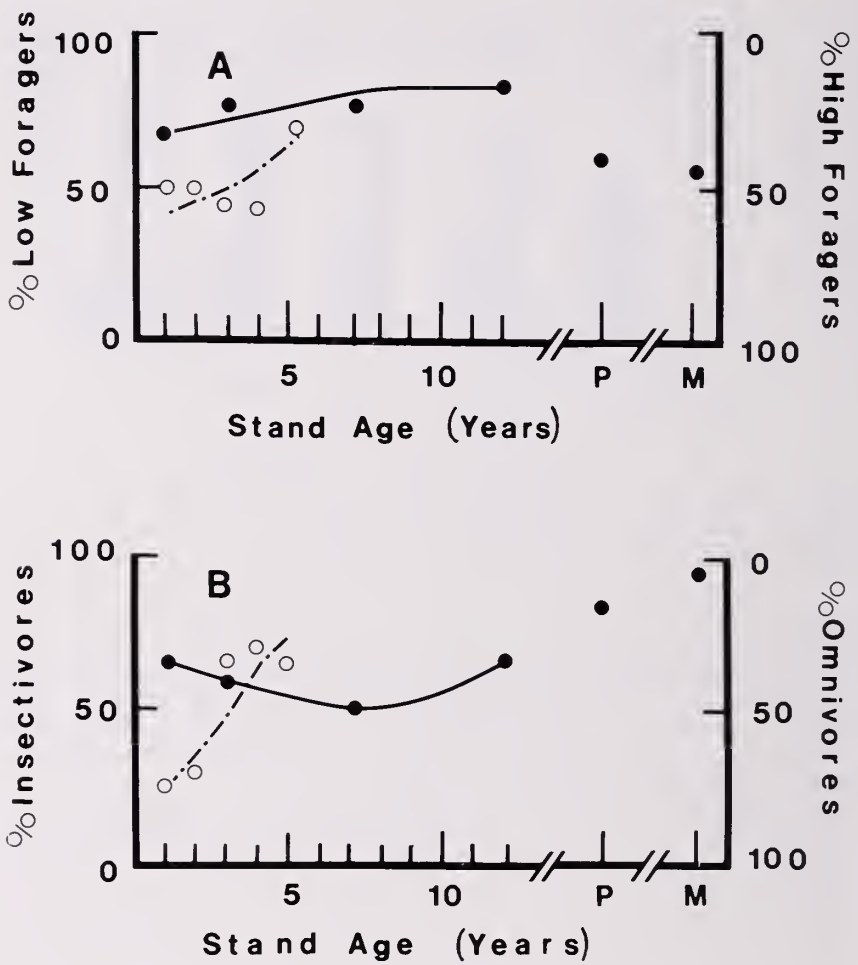

FIG. 3. Percentage of individuals in food guilds at various clearcuts. A: Low vs high foragers. B: Insectivores vs omnivores. Open circles and dashed lines indicate Highlands sites; closed circles and solid lines are data from southwestern Virginia (Conner and Adkisson 1975). P = pole stand, M = mature stand.

more time within the rapidly developing vegetation. Some (such as Tufted Titmouse and Hooded Warbler at 5-year-old Horse Cove) actually established territories in these older areas.

A paucity of birds at the first-year site was quite evident; only three species bred there, presumably because of the lack of vegetation during the period of establishment of territories. As regrowth occurred later in the season, some species occasionally foraged there.

Changes in the diversity index were positively correlated with time since logging (Fig. 1). These results parallel those of Conner and Adkisson (1975) who found generally higher

values for H′ for all years of their study, perhaps due to a larger logged area and greater species pool. Several of their more numerous bird species were not found within the Highlands area. Their work, extending over a greater range of site ages, suggested a diversity peak after about 12 years of regrowth.

With increasing site age there was a statistically significant increase in the numbers of thicket-nesting individuals and a concurrent decrease in ground nesters ($\chi^2 = 49.57$, df = 8, $P < 0.001$; Fig. 2). This may have resulted from increasing diversity of above-ground nesting habitats as plant regeneration proceeded. Only slash piles and small sprouts provided cover at the first-year site; few species of birds nested there. Regrowth was rapid and dense, suitable for more thicket nesters during succeeding years. Cavity nesters were irregular and dependent on the presence of snags (Conner and Crawford, J. For. 72:564–566, 1974; Conner et al., J. Wildl. Manage. 39:144–150, 1975), few of which were in any of the areas studied. Woodpeckers occasionally visited the clearcuts, but only the Common Flicker (*Colaptes auratus*) regularly foraged there.

Food guild changes were more complex. The number of birds which typically forage in low vegetation showed a significant increase with site age ($\chi^2 = 43.83$, df = 4, $P < 0.001$), achieving numbers nearly as high as those derived from data of Conner and Adkisson (1975) (Fig. 3A). Insectivores were clearly more abundant in older than younger cuts at Highlands ($\chi^2 = 94.12$, df = 4, $P < 0.0001$; Fig. 3B). The early stages of regrowth contained many annuals and biennials not found in mature stands (Horn 1980). This greater seed source evidently made young clearcuts more attractive to omnivores.

One problem with this study was the lack of replicate sites. Observed changes in diversity and guild structure may have been the result of intersite differences, rather than time since logging. Without replication of study areas the time/site interaction is difficult to distinguish statistically, particularly over such a short regeneration sequence. The spot-map method is a time-consuming process, making replication difficult in dense second-growth forests. For such studies it may be more advantageous to use strip transects (Emlen, Auk 94:455–468, 1977; Conner and Dickson, Wildl. Soc. Bull. 8:4–9, 1980).

In summary, clearcutting can yield significant short-term changes in both diversity and guild structure of bird communities. As indicated earlier, one forest management goal has been to maximize diversity. Clearcutting apparently creates greater habitat diversity than selective cutting (Franzreb and Ohmart, Condor 80:431–441, 1978). Habitat diversity can also be increased by clearcutting adjacent areas at different times, resulting in a range of age and area classes (Boyce, USDA For. Serv. Resear. Pap. SE-168, 1977; Boyce and Cost, USDA For. Serv. Resear. Pap. SE-194, 1978). As I have shown here, there are also significant changes in community guild structure. Further research, thus, should be designed to examine both numerical and behavioral changes.

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Roost habitat selection by three small forest owls.—In 1981 we examined winter and spring roost sites of Boreal (*Aegolius funereus*) and Saw-whet (*A. acadicus*) owls and late winter, spring, and summer roosts of Screech Owls (*Otus asio*) in the River of No Return Wilderness, Idaho. Characteristics of the vegetation around the roost site, as well as the position of the owl in the tree, were used to compare the roosting habits of these three small forest owls.

Study area and methods.—The study was conducted at two sites in the River of No Return Wilderness, Idaho (45°22′N, 115°07′W). Screech and Saw-whet owls were located near Taylor Ranch along Big Creek at 1175 m elevation. Douglas fir (*Pseudotsuga menziesii*) forest dominates northern aspects whereas bunchgrass, mountain shrub, and open Douglas fir habitats are interspersed on the dryer aspects. The riparian zones vary from stands of large Douglas fir with little understory to dense deciduous cover of birch (*Betula occidentalis*), alder (*Alnus tenuifolia*), hawthorn (*Crataegus* sp.), and scattered black cottonwood (*Populus tricocarpa*).

Boreal and Saw-whet owls inhabited the second study site near Chamberlain Basin Ranger Station at 1720 m elevation. Lodgepole pine (*Pinus contorta*) predominates; however, uneven-aged stands of mixed ponderosa pine (*P. ponderosa*), Douglas fir, and lodgepole pine occupy some slopes. Climate, vegetation, and topography of the region are discussed in more detail by Hornocker (Wildl. Monogr. No. 21, 1970) and Hayward (M.S. thesis, Univ. Idaho, Moscow, Idaho).

Boreal, Saw-whet, and Screech owls captured in bal-chatri traps or mist nets and radio tagged, were located on their diurnal roosts. The position of the owl in the roost tree was recorded by height above ground (estimated with a clinometer), distance from bole, and distance to nearest branch above and below the roost. The amount of cover afforded the owl by vegetation above, to the sides, and below the roost was rated on a scale from 1–5 for each direction. Both the density of vegetation and distance to the protective cover were used in assigning the cover rating.

The roost tree was later characterized by height, dbh, and minimum canopy height. Timber density within concentric 5.2-m and 11.4-m radius circles around the roost tree was recorded for trees in four size classes: 2.5–7.6, 7.6–23, 23–53, and >53 cm dbh. A modified line intercept sample totaling 360 m was used to characterize the structure of surrounding vegetation (Mueller-Dombois and Ellenberg, Aims and Methods of Vegetation Ecology, John Wiley & Sons, New York, New York, 1974). We measured the portion of eight lines, radial to the roost, intercepted by five vegetation cover categories. Lines in the four cardinal directions were each 60 m long; the remaining four lines were each 30 m. Data were tested for normality. Those variables deviating significantly from a normal distribution were transformed and retested. Statistical tests were performed on the transformed data.

Results.—We located the roosts of one Boreal Owl (N = 13) between 26 January and 8 April, two Screech Owls (N = 13) between 11 February and 5 August, and three Saw-whet Owls (N = 15) between 12 March and 22 June. Only a single Boreal Owl roost occurred in a cavity; on all other occasions owls roosted in conifers or shrubs. Only Screech Owls showed repeated use of roosting perches. One Screech Owl used the same roost on three of four occasions. Seven pellets found under one Boreal Owl roost, however, indicated repeated use by this bird. Roosts of Boreal and Saw-whet owls were dispersed, separated by as much as 2 km and 1.8 km, respectively, on consecutive days.

All roost trees of the Boreal Owl were coniferous, and its home range had less than 2% deciduous cover. Home ranges of all three Saw-whet Owls were bisected by stream courses

TABLE 1
MEAN (± SE) CHARACTERISTICS OF ROOSTS OF SMALL FOREST OWLS

Characteristic	Owl species		
	Boreal	Saw-whet	Screech
Roost height (m)	6.9 (±0.60)	4.2 (±0.64)	4.60 (±1.46)
Min. roost height (m)	2.7	0.9	0.60
Max. roost height (m)	10.7	7.3	12.20
Roost tree height (m)	19.4 (±1.62)	22.6 (±3.04)	21.20 (±4.64)
Bole height (m)	5.2 (±0.90)	1.8 (±0.27)	2.31 (±0.99)
DBH of roost tree (cm)	36.0 (±5.84)	46.0 (±8.20)	54.00 (±14.35)

and associated deciduous riparian habitat. A single Saw-whet Owl roost was found in a deciduous thicket; all others occurred in coniferous trees. Both Screech Owls concentrated their activity along Big Creek where conifer and deciduous habitats are mixed. Prior to leafout in spring, only conifers were used; however, after leafout, 45% of the Screech Owl roosts were in deciduous trees.

Over 80% of the Boreal and Screech owls perched immediately next to the bole of the roost tree. In contrast, 54% of the Saw-whet Owl roosts were >1 m from the bole. Saw-whet Owls often perched within foliated portions of the tree on the outer half of the branch.

The protection offered the roosting owl by surrounding foliage appeared to differ between species. The Boreal Owl was much easier to find on its roost than the Saw-whet or Screech owls. After locating the roost tree using the radio signal, we could usually find the Boreal Owl within 10 min; finding Saw-whet and Screech owls took up to 45 min. Nonparametric ANOVA (Kruskal-Wallis test) of the cover rating above, below, and to the side of the roost indicated a difference between species in protection above the roost ($P = 0.054$). Boreal Owl roosts had the least protection from above, and Saw-whet Owl roosts the most protection. There was no significant difference among species in distances to the nearest branch above or below the roost (ANOVA; $P = 0.16$ above, and $P = 0.21$ below). Saw-whet Owls roosted significantly lower in the tree than Boreal Owls ($P < 0.05$, Table 1).

Within a 5.2-m radius circular plot around the roost, tree density was higher for Boreal Owls (152 ± 22.8 trees/0.1 ha [$\bar{x}$ ± SE]) than Screech Owls (106.2 ± 58.4 trees/0.1 ha) or Saw-whet Owls (78.2 ± 36.5 trees/0.1 ha). This same pattern was seen in concentric circular plots extending from 5.2–11.4 m from the roost where tree density was highest around Boreal Owl roosts (90.7 ± 13.7 trees/0.1 ha), less around Screech Owl roosts (40.2 ± 30.5 trees/0.1 ha), and least around Saw-whet Owl roosts (30 ± 11.7 trees/0.1 ha). Multivariate ANOVA, by study site, however, demonstrated that the apparent greater timber density around Boreal Owl roosts may result from differences in habitat at Chamberlain Basin and Taylor Ranch rather than differences in roost selection by the owl species. Boreal Owls chose roosts with denser timber within 5.2 m of the roost than in the next 6 m (paired-t test, $P = 0.001$). For the Saw-whet and Screech owls, the higher timber density near the roost was not significant (paired-t test, $P = 0.09$ for both species). Analysis of the vegetation cover (proportions of major categories) within a 60-m radius of the roost showed no significant overall differences among owl species (MANOVA $P = 0.11$ at Taylor Ranch, $P = 0.14$ at Chamberlain).

Discussion.—Roosts chosen by Boreal, Saw-whet, and Screech owls were similar in that virtually all owls perched in trees rather than using cavities, and tree density immediately around the roosts was greater than in the adjacent forest. Roosts of these species differed in the amount of cover which the roost trees provided and the positions of the perches on the branches. The pattern of roost selection suggests that roosts are chosen to provide both thermal and hiding cover. The small Saw-whet Owl, which would be most vulnerable to predation by accipiters, chose the most concealed roosts by perching in the foliage toward the end of the branch. Such a location may be energetically more costly than near the tree bole because of increased convective heat loss (Walsberg and King, Wilson Bull, 92:33–39, 1980). The larger Boreal and Screech owls, whose silhouettes would be more conspicuous far out on the branch, roosted next to the tree trunks where their cryptic plumage matched the tree bark. None of the owls perched on the unprotected area between the bole and the foliage where they would be highly visible.

Balda et al. (Auk 94:494–504, 1977) suggest that species commonly roost in situations similar to their nest-site, species which nest in cavities or domed nests selecting similar roost situations. Why didn't the Boreal, Saw-whet, and Screech owls roost in cavities when snags were plentiful in the unharvested forest? Perhaps owls consistently roost in cavities only when sufficient protective cover for concealment is not available. VanCamp and Henny (U.S. Dept. Interior Am. Fauna Ser. No. 71, 1975) reported that Screech Owls in deciduous forests began roosting in nest boxes during October when leaf fall would make a roosting owl most conspicuous. Perhaps a cavity roosting owl is protected from aerial predators but vulnerable to marten (*Martes americana*) or other arboreal mammals. Roosting under a conifer, however, may provide adequate concealment from hawks and other owls and the opportunity to escape approaching mammalian predators.

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Distribution of wintering Golden Eagles in the eastern United States.—The Golden Eagle (*Aquila chrysaetos*) is the most widely distributed and, perhaps, the most numerous of the world's "large" eagles (Brown and Amadon, Eagles, Hawks and Falcons of the World, Vol. 2, McGraw-Hill, New York, New York, 1968). The North American subspecies (*A. c. canadensis*) is most abundant west of the Great Plains from northern Alaska into central Mexico (Boeker, Wildl. Soc. Bull. 2:46–49, 1974). A remnant breeding population has persisted at least until recently in the Adirondack Mountains and Maine (Spofford, Am. Birds 25:3–7, 1971), and the species apparently continues to breed, albeit sparsely, in remote parts of eastern Canada (Snyder, Can. Field-Nat. 63:39–41, 1949; Spofford 1971; Peck and James, Breeding Birds of Ontario. Nidiology and Distribution, Vol. 1: Nonpasserines, Royal Ont. Mus. Publ. Life Sci., Toronto, Ontario, 1983). A few Golden Eagles are observed each winter in subarctic and temperate sections of eastern North America (e.g., Edwards, Chat 26:19, 1962; Daley, Passenger Pigeon 25:5, 1963; Kelly, Jack-Pine Warbler 50:53–61, 1972; Adkisson et al., Raven 49:32–33, 1978).

The winter distribution of Golden Eagles in eastern North America remains poorly understood. The National Wildlife Federation's (NWF) Raptor Information Center has sponsored

TABLE 1

GOLDEN EAGLE OBSERVATIONS FROM NATIONAL WILDLIFE FEDERATION MIDWINTER EAGLE SURVEY BY STATE, 1979–1982[a]

State[b]	No. Golden Eagle sightings			
	1979	1980	1981	1982
Alabama	1	2	2	2
Delaware	1	1	0	0
Georgia	4	0	0	0
Illinois	2	2	1	0
Kentucky	4	9	7	4
Maryland	2	6	3	2
Massachusetts	0	1	0	2
Michigan	2	1	1	1
Mississippi	1	0	2	1
New Jersey	2	0	1	2
New York	0	0	0	1
North Carolina	3	0	0	0
Pennsylvania	0	4	0	1
South Carolina	1	0	3	0
Tennessee	12	6	2	15
Vermont	0	1	0	0
Virginia	0	0	0	3
West Virginia	1	0	0	0
Wisconsin	0	0	0	1
Total	36	33	22	35

[a] Surveys were conducted each year in all eastern states except Florida.

[b] No Golden Eagles were reported on midwinter surveys in Connecticut, Indiana, Maine, New Hampshire, Ohio, and Rhode Island.

a midwinter eagle survey throughout the contiguous United States since 1979. This survey has provided the most complete information to date on the winter distribution of Golden Eagles throughout the survey region. The purpose of this note is to summarize midwinter eagle survey data and other published information on wintering Golden Eagles in the eastern United States, and to describe distributional trends and identify regular wintering areas.

Methods.—The NWF midwinter eagle survey represents a coordinated effort, involving state and federal biologists and volunteers, to count Bald Eagles (*Haliaeetus leucocephalus*) and Golden Eagles throughout the coterminous United States during a 2–3-week period in January. The primary purpose of the survey is to count as many Bald Eagles as possible, but participants also actively count Golden Eagles in all states but Florida. Surveys in most cases are not systematic or standardized. Data used in this paper are from surveys from 1979–1982. Surveys were conducted from 13–27 January in 1979, from 2–20 January in 1980, and from 2–16 January in 1981 and 1982. Survey participants characteristically searched for eagles on foot, by vehicle, by boat, from fixed-wing aircraft, and/or by helicopter in as many areas as possible and reported sightings and areas searched to a regional coordinator using standardized survey forms. These reports were edited by regional coordinators to eliminate duplicate sightings and forwarded to the NWF for compilation. Although the

midwinter survey is relatively complete compared with previous efforts, in all years counts were conducted in fewer than 50% of the counties in the eastern United States and survey coverage was heavily weighted toward habitats likely to support Bald Eagles. As a result many Golden Eagle wintering areas were probably overlooked.

To supplement midwinter survey data, most local, regional, and national ornithological journals, as well as Bird-Lore (1919–1940), Audubon Magazine (1941–1946), Audubon Field Notes (1947–1970), and American Birds (1973–1981) were searched for occurrence records. Records used spanned the period 1853–1981. About 16% of the records used in this analysis were from the NWF midwinter eagle survey; the remaining 84% were from published literature.

For the purposes of this review we defined the eastern United States as the area east of the Mississippi River; we did not include sightings directly on the river, or sightings from eastern Louisiana and eastern Minnesota. These areas were excluded because Golden Eagles observed on the Mississippi River during midwinter eagle surveys were not always reported, and only a few counts were conducted away from the river in eastern parts of these states. Data were summarized by physiographic region after Brown and Kerr (Bureau of Land Manage. Physiographic Regions, Am. Geogr. Soc., Spec. Publ. No. 36, 1979). We defined the winter period as 1 December–15 March.

Owing to the volume of published material used (216 references), specific dates, locality information, and literature citations are not given for each record of occurrence. This information, as well as additional unpublished material on the midwinter eagle survey, is available upon request from the senior author.

Results and discussion.—Our review of the literature and midwinter eagle survey data resulted in a total of 613 winter Golden Eagle records of occurrence in the eastern United States during the 129-year period (1853–1982). Several other records lacking sufficient locality data for inclusion were also found.

NWF midwinter eagle surveys have resulted in an average of 31.5 (SE = 3.2) sightings annually (Table 1), although the actual number of Golden Eagles present was probably greater in each year because survey coverage was always incomplete. Counts of autumn migrants also suggested that higher numbers of Golden Eagles may be present in the eastern United States in winter, assuming that these migrants remain in the east. For example, for the period 1946–1970 an average of 42 Golden Eagles was counted each autumn at Hawk Mountain, Pennsylvania, and up to 80 have been counted there in a single year (Spofford 1971). Spofford (1971) also pointed out, however, that the Hawk Mountain counts have declined gradually throughout this period: between 1965–1970 Golden Eagle counts averaged only 29 per year.

Winter Golden Eagle records were not uniformly distributed throughout the eastern United States. Most sightings were concentrated within or along the southwest border of the Appalachian Plateau physiographic region (30.1% of all records) and within the Coastal Plain physiographic region (33.3% of all records) (Fig. 1). Midwinter eagle survey data show a similar distributional pattern. Relative abundance of Golden Eagles (calculated for each year of the survey as the number of individuals observed per 1°-block divided by the number of localities searched in the 1°-block) was highest in the Tennessee River valley in western Tennessee, near the confluence of the Ohio and Mississippi rivers, in the Chesapeake Bay area, and along the Mississippi River plain in northern Mississippi (Fig. 2).

Of 126 Golden Eagles reported on midwinter surveys from 1979–1982, age (adult or immature) was determined for 93: 40 were immature and 53 adult. Although the ratio of immatures to adults in the full sample did not deviate significantly from 1:1 (χ^2 goodness of fit test: $\chi^2 = 1.05$, df = 1, NS) there was a significant departure from uniformity across

FIG. 1. Winter Golden Eagle occurrence records from 1853–1982 in the eastern United States by physiographic region (after Brown and Kerr 1979). Each small dot represents <5 records; larger circles represent regularly used winter areas (see Table 3) and indicate ≥5 records. Letters denote physiographic regions, where A = Coastal Plain, B = Mississippi Delta and Plains, C = Appalachian Plateau, D = Central Lowland, E = New England Plateau, and F = Lake Plains.

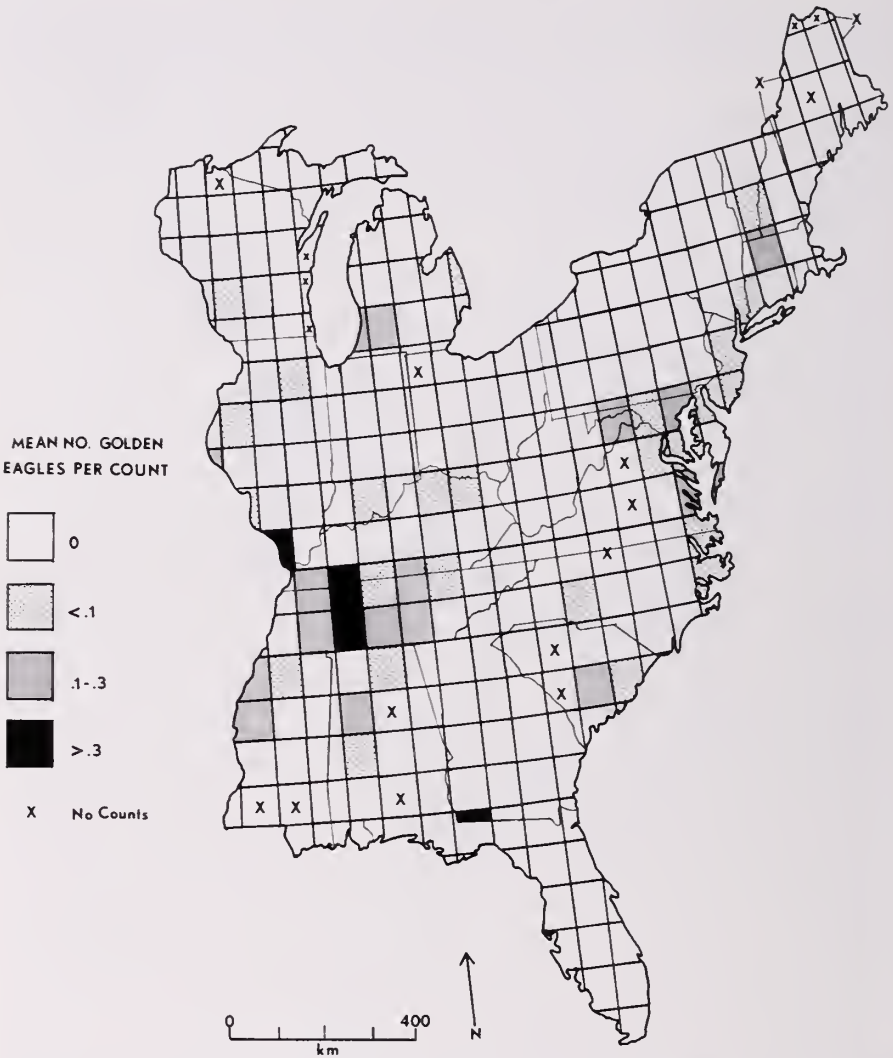

FIG. 2. Distribution and relative abundance of wintering Golden Eagles by 1°-latitude-longitude block, as determined from National Wildlife Federation midwinter eagle survey, 1979–1982. Relative abundance was calculated for each year as the number of Golden Eagles observed (excluding duplicate sightings) in each 1°-block divided by the number of counts conducted (number of localities searched) within the 1°-block. No counts were conducted in the state of Florida, or in 1°-blocks marked with an X.

TABLE 2

AGE DISTRIBUTION OF GOLDEN EAGLES SEEN IN MIDWINTER EAGLE SURVEYS, 1979–1982[a]

Year	% immatures (N) by physiographic region		
	Coastal plain	Appalachian plateau[b]	Central lowland[c]
1979	100.0 (1)	80.0 (5)	—
1980	75.0 (8)	40.0 (5)	40.0 (15)
1981	60.0 (10)	33.3 (3)	33.3 (9)
1982	53.3 (15)	25.0 (4)	11.1 (18)
Years combined[d]	61.8 (34)	47.1 (17)	26.2 (42)

[a] Age (adult or immature) was determined by plumage characteristics (Brown and Amadon 1968). Golden Eagles reported as age unknown (33) were excluded from calculations.

[b] Includes one record from the New England Plateau Physiographic Region.

[c] Includes four records from the Lake Plains Physiographic Region. No Golden Eagles were reported in this region in 1979.

[d] χ^2 goodness of fit test of the distribution of sightings of immature Golden Eagles across regions led to rejection of the null hypothesis of uniformity ($\chi^2 = 15.87$, df = 2, $P < 0.001$).

physiographic regions (Table 2). In general, survey data show that the proportion of immature Golden Eagles in counts declined from the Coastal Plain inland. The use of different wintering areas by adults and immatures of the same species is not uncommon among large eagles; e.g., adult Bald Eagles and adult Steppe Eagles (*Aquila rapax*) winter farther north than immatures (Sprunt and Ligas, pp. 25–30 *in* Proc. 62nd Natl. Audubon Soc. Ann. Conf., 1966; Brooke et al., Occ. Pap. Natl. Mus. Rhodesia B5:61–114, 1972). Erskine (Auk 85: 681–683) suggested that, at least for the Bald Eagle, partial segregation of adults and immatures on the winter range lessens intraspecific competition for food. Assuming observed geographic differences in age ratio for the Golden Eagle are not artifacts of the small sample size, the tendency for immatures to winter in greater numbers near the coast may be equivalent to the use of low latitudes by immature Bald and immature Steppe eagles since proximity to the ocean moderates the climate of the Coastal Plain (Shelford, The Ecology of North America, Univ. Illinois Press, Urbana, Illinois, 1963).

Habitat information was available for 245 of the total 613 records, and of these, 201 (82.0%) were associated with riverine or wetland systems. Most inland records were from steep river valleys or associated reservoirs and marshes. On the coast, estuarine marshlands, barrier islands and associated sounds, and the mouths of major river systems accounted for most records. Eleven of 23 regularly used wintering sites (five or more records over three or more years) were on wildlife management areas that, according to Bellrose (Ducks, Geese and Swans of North America, Stackpole Books, Harrisburg, Pennsylvania, 1976), attract considerable numbers of waterfowl and other wetland species (Table 2). Wetland management areas are probably visited more than upland management areas or private lands by persons likely to report Golden Eagle sightings owing to the accessibility and high wildlife values of these areas; thus, these results may be misleading. Nevertheless, the occurrence records do show that activities on many managed wetlands have been conducive to winter use by Golden Eagles. Three factors may contribute to the attractiveness of managed wetlands: (1) a dominance of open vegetation; (2) large, concentrated prey populations; and (3) absence of harassment and reduced human disturbance.

Sanders (pp. 109–110 *in* Proc. Fire by Prescription Symp., Atlanta, Georgia, 1976) re-

TABLE 3

REGULAR WINTERING SITES[a] OF GOLDEN EAGLES IN THE EASTERN UNITED STATES

State County	Location	Span of records	Total no. of records
Alabama			
Barbour	Eufaula NWR[b]	1975–1978	5
Morgan/Limestone	Wheeler NWR	1974–1981	5
Florida			
Alachua	Not specified	1928–1981	5
Wakulla	Wakulla Springs	1960–1978	7
Georgia			
Quitman	Eufaula NWR	1975–1980	5
Ware	Okefenokee NWR	1958–1976	6
Illinois			
Williamson	Crab Orchard NWR	1957–1980	5
Kentucky			
Ballard	Ballard Co. WMA[c]	1979–1981	12
Trigg/Lyon	Land Between the Lakes	1967–1980	9
Maryland			
Dorchester	Blackwater NWR	1954–1981	17
Kent	Eastern Neck NWR area	1962–1981	9
Massachusetts			
Essex	Not specified	1931–1974	14
Franklin/Worcester	Quabbin Reservoir	1973–1980	9
Michigan			
Allegan	Allegan NWR area	1972–1980	5
New Jersey			
Atlantic	Brigantine NWR	1975–1979	6
New York			
Dutchess/Ulster	Not specified	1969–1981	13
North Carolina			
Dare	Pea Island NWR	1951–1953	5
Pennsylvania			
Berks	Hawk Mountain area	1960–1977	7
South Carolina			
Charleston	Not specified	1950–1968	6
Tennessee			
Benton/Humphreys	Tennessee NWR	1952–1979	19
Cannon/DeKalb	Not specified	1968–1980	17

TABLE 3
CONTINUED

State County	Location	Span of records	Total no. of records
Virginia			
Montgomery	Jefferson NF[d]	1911–1980	5
West Virginia			
Pendelton	Not specified	1976–1981	10
Wisconsin			
Burnett	Crex Meadows NWR	1963–1977	7
Total			278

[a] Regularly used wintering areas were sites with five or more records over 3 or more years.
[b] NWR = National Wildlife Refuge.
[c] WMA = Wildlife Management Area.
[d] NF = National Forest.

ported that montane grass and heath balds (naturally occurring treeless areas below the climatic treeline in otherwise forested areas) are also important to wintering Golden Eagles for foraging, based upon his observations in the Appalachian Plateau physiographic region in North Carolina. Although only a small proportion (1.8%) of the 613 records used in this study were explicitly associated with montane balds, this figure may be misleading as this ecosystem is comparatively inaccessible and less subject to casual observation than valley and coastal wetlands. Further research is needed to elucidate the relative importance of montane bald ecosystems to wintering Golden Eagles.

There are five eastern recoveries of Golden Eagles banded as nestlings. All were from natal areas in eastern North America, and all were recovered in autumn or winter in the eastern United States or southeastern Canada (Fig. 3). Only one was recovered after its first year (at 18 months of age). These records support arguments by Snyder (1949) and Spofford (Bird-Banding 35:123–124, 1964) that the principal source of Golden Eagles that winter in the eastern United States is the northeastern Canadian Arctic and, to a lesser degree, the far northeastern United States. Smith (Redstart, July:94–97, 1982) mentions the possibility that another source may be northwestern Canada. While data are too sparse to rule out this possibility, it is of interest to note that of 275 nestling Golden Eagles banded in western North America that have been recovered, none have been found east of the Mississippi River (U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Bird Banding Laboratory, pers. comm.).

Several authors have speculated that Golden Eagle populations have decreased considerably within the last century in eastern North America (Bent, U.S. Natl. Mus. Bull. 167, 1937; Spofford 1971; Smith 1982). Although the actual extent and history of the population may never be known, comparatively recent data suggest the eastern breeding population may indeed be declining (Spofford 1971; Singer, N.Y. Fish and Game J. 21:19–31, 1974). While maintenance of habitat integrity in existing breeding areas is important if current population levels are to be sustained or increased, the availability of sufficient wintering habitat is equally important.

To date there has been little intentional management of Golden Eagle breeding or wintering

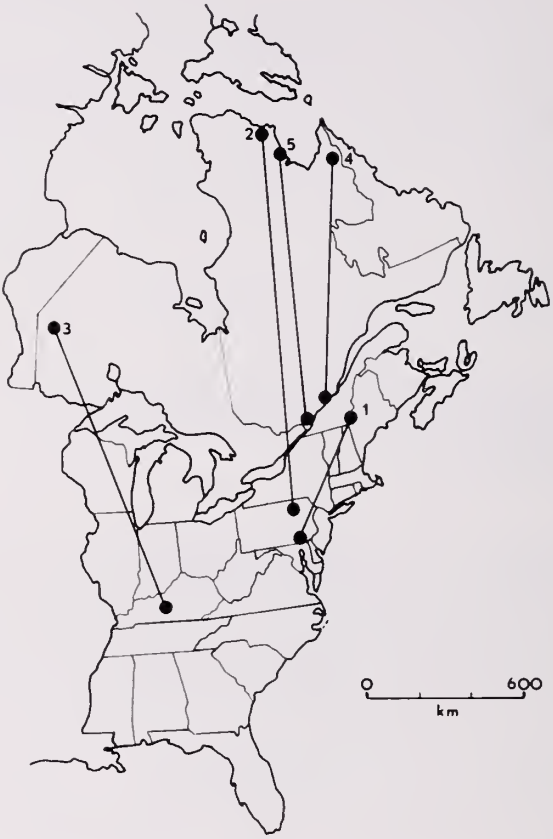

FIG. 3. Natal and recovery sites of banded nestling Golden Eagles recovered in eastern North America. Nestling no. 1 was banded on 10 July 1963 and was found dead in November 1963 (Spofford 1964). Nestling no. 2 was banded on 26 July 1967 and was recaptured and released on 23 October 1967 (Spofford 1971). Nestling no. 3 was banded on 28 June 1978 and was found dead in December 1979. Nestling no. 4 was banded on 7 July 1969 and was found shot in October 1969. Nestling no. 5 was banded on 8 August 1972 and was found in a trap on 20 January 1973.

habitat in eastern North America. One notable exception is the work in North Carolina by the U.S. Forest Service to maintain physiognomic characteristics of montane bald ecosystems through prescribed burns (Sanders 1976). Nevertheless, data presented in this paper suggest that intensive waterfowl management programs involving the acquisition, reclamation, and management of wetlands may have indirectly benefitted Golden Eagles, although the association may not be entirely positive. Bald Eagles that winter in waterfowl concentration areas open to hunting with lead shot are susceptible to secondary lead poisoning (Griffin et al., Trans. N. Am. Wildl. Nat. Resour. Conf. 45:252–262, 1980: Hoffman et al., J. Wildl. Disease 17:423–431, 1981), and nationwide, Bald Eagle mortality from lead toxicosis may

be substantial (Pattee and Hennes, Trans. N. Am. Wildl. Nat. Resour. Conf. 48:230–237, 1983). Golden Eagles regularly feed on waterfowl and carrion (Sherrod, Raptor Resear. 12: 49–121), and individuals that winter at waterfowl concentration areas where lead shot is used probably feed on moribund and dead ducks and geese. Secondary lead poisoning may be a significant cause of mortality for this species as well.

Acknowledgments.—The NWF midwinter eagle survey was coordinated from 1979–1981 by M. E. Pramstaller, and the survey data used in this analysis resulted from his efforts on this project as well as the efforts of the regional coordinators and several thousand dedicated volunteers. R. W. Fyfe, J. W. Grier, and W. R. Spofford graciously permitted the use of information on band recoveries, and M. R. Fuller was instrumental in making this information available. We would like to thank K. W. Ballard, G. R. Bortolotti, W. S. Clark, K. W. Cline, M. W. Collopy, M. R. Fuller, R. S. Kennedy, M. N. LeFranc, Jr., S. D. Miller, and W. A. Wentz for critically reviewing the manuscript, as well as R. Hudson for typing the manuscript.—Brian A. Millsap and Sandra L. Vana, *Raptor Information Center, Institute for Wildlife Research, National Wildlife Federation, 1412 Sixteenth Street, N.W., Washington, D.C. 20036.* *Accepted 27 Aug. 1984.*

Wilson Bull., 96(4), 1984, pp. 701–705

Some factors affecting productivity in Abert's Towhee.—Abert's Towhee (*Pipilo aberti*) is restricted to desert riparian zones of Arizona and bordering states (Phillips et al., The Birds of Arizona, Univ. Arizona Press, Tucson, Arizona, 1964). Its breeding behavior, communication, and physiological responses have been detailed by Marshall (Condor 62:49–64, 1960; pp. 620–622 *in* Proc. XIII Int. Ornithol. Congr., Ithaca, New York, 1962; Condor 66:345–356, 1964), and Dawson (Univ. Calif. Publ. Zool. 59:81–124, 1954), but no information is available on annual productivity. Abert's Towhee is multibrooded, and therefore, the number of broods per season as well as nesting success and clutch-size contribute to productivity. My objectives were to describe the productivity of Abert's Towhee in 1980 and to quantify seasonal variation in length of nesting, a factor that affects productivity. I have documented elsewhere (Finch, Condor 85:355–359, 1983) the effects of changing rates of brood parasitism on the nesting success of Abert's Towhee.

Methods.—During the summer of 1979, I established a 20-ha grid in honey mesquite (*Prosopis glandulosa*) habitat 10 km N of Ehrenberg, Yuma Co., Arizona. From January–July 1980, 15 h each week were spent looking for nests on, or near, the study grid. Nests were inspected between 10:00 and 12:00 every 2 or 3 days. Fieldwork terminated in July when no new nests were initiated.

From May–August 1979, I mist-netted and color-banded Abert's Towhees, of which eight were adults. Five banded adult females were present in the breeding population the following year. In 1980, I color-banded 12 more females.

Annual productivity, which is the number of fledglings produced in one year, can be estimated from the expression (Ricklefs, pp. 336–435 *in* Breeding Biology of Birds, D. S. Farner, ed., Natl. Acad. Sci., Washington, D.C., 1973): (no. eggs/clutch·no. nesting attempts·% success)/2 adults/pair. The number of nesting attempts was measured directly by following marked females throughout their breeding cycle. To increase sample size, I also used nesting data for unmarked birds and estimated the number of attempts indirectly by dividing the length of the season by the time required for each nesting attempt (Ricklefs 1973). The length of a nesting attempt is approximated by the equation (Ricklefs 1973): $T = P(t + r_s) + Q(t_f + r_f)$, where T = average length of a nesting attempt, P = proportion of nestings that succeed, Q = 1 − P, proportion of nestings that fail, t = combined average

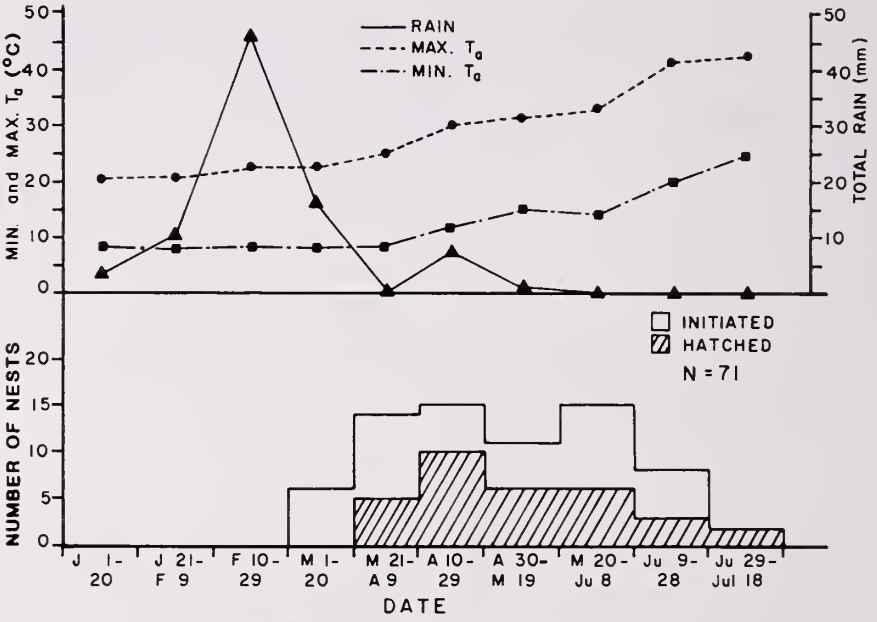

FIG. 1. Nest initiation in relation to patterns of air temperature (T_a) and total rainfall.

length of laying, incubation, and nestling periods, t_f = average time to failure in an unsuccessful nest, and r_s, r_f = time before initiation of a new nest after a success and a failure, respectively (estimated from marked birds). The number of attempts during the year was calculated as length of season divided by T. Using Ricklefs (1973) methods, season length was estimated from MacArthur's (Am. Nat. 98:387–397, 1964) index: $e^{-\Sigma p_i \ln p_i}$, where p_i is the proportion of all nests that are started during the time interval i. Multiplying the index by the time interval (in this case 20) converted it into days.

The success of nest contents was calculated by Mayfield's (Wilson Bull. 73:255–261, 1961; Wilson Bull. 87:456–466, 1975) method. Johnson's (Auk 96:651–661, 1979) statistic was used to test for differences between daily success rates ($\hat{s}$) of incubation and nestling phases.

Maximum and minimum air temperature and precipitation data that approximate conditions in the study area were obtained from the Palo Verde Irrigation District weather station, Blythe, Yuma Co., California, located about 25 km SW from the study area.

Results.—Abert's Towhees began building nests on the study area in early March 1980. Air temperatures during this period averaged 23.9°C maximum and 8.3°C minimum (Fig. 1). Air temperatures averaged 42.9°C maximum and 24.8°C minimum in July when towhees terminated breeding. Over a 20-year period, the greatest monthly precipitation usually occurred in July, and the average rainfall in February was 8.1 mm (Anderson et al., USDA For. Serv. Gen. Tech. Rept. RM-43:183–192, 1977). However, 1980 was atypical, with no precipitation in June and July and with the peak rain falling in February (46.2 mm) (Fig. 1).

Abert's Towhees began breeding approximately 2 weeks after the peak in February rains (Fig. 1). The earliest clutch was initiated (i.e., first egg laid) on 13 March. Because it takes

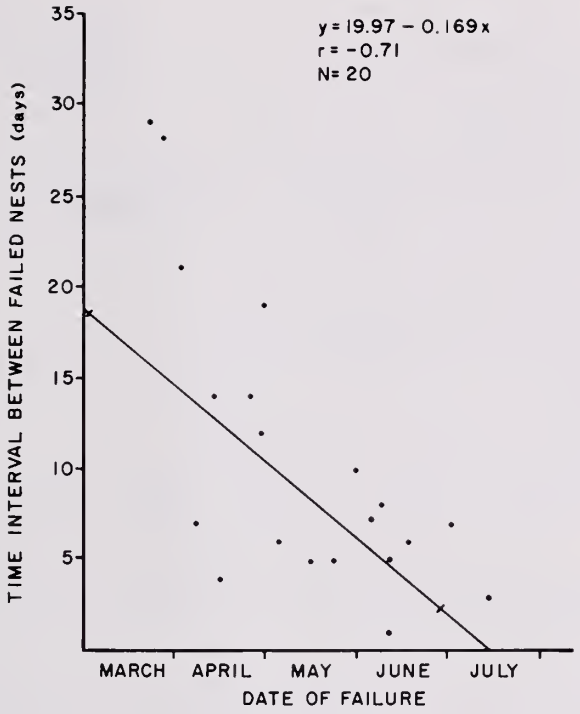

FIG. 2. Time intervals between nest failure and first egg laid in new nest of banded females.

towhees at least a week to construct their first nest, nest building was probably initiated in the first week of March. Mean clutch-size was 2.85 eggs (N = 65, SE = ±0.35, range 1–4, mode = 3). Females began incubating shortly after the first egg was laid. Hatching was asynchronous (up to a day apart) after an incubation period of 14 days. Nestlings fledged at 12–13 days of age. The total length of a successful nesting cycle (t_s), excluding time involved in nest building and post-fledging stages, was approximately 30 days.

Fledglings were attended by both parents 4–5 weeks before they attained independence. The time interval between fledging of young and laying of the first egg in a new nest (r_s) was approximately 42 days (i.e., 5 weeks of fledgling dependency plus 1 week to build a new nest). The time interval required by a female before she laid the first egg of a new clutch after a failed clutch, significantly decreased with time of season ($r = -0.71$, $P < 0.01$, N = 20) (Fig. 2). There was also a decrease in the time interval between new nest construction and first egg laid in a new nest ($r = -0.9$, $P < 0.01$, N = 10). The average time before initiation of a new nest after a failure (r_f) was 10.06 days (N = 18, two nests excluded from computation because new clutches were laid in old nests). A decline in r_s (time before nest initiation after a success) over the breeding season, if present, (e.g., Kluyver et al., pp. 153–169 *in* Evolutionary Ecology, B. Stonehouse and C. M. Perrins, eds., Univ. Park Press, London, England, 1977) could not be detected because of insufficient data.

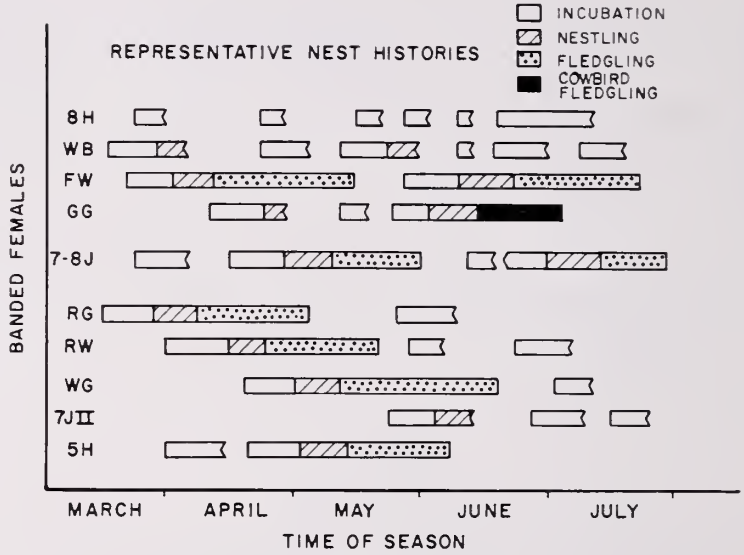

FIG. 3. Representative nesting histories of banded female Abert's Towhees. Bars with squared-off ends signify successful completion of nest cycle. Bars with indented ends represent failed nests. Female identifications are given in column on left side of figure.

The length of time a nest was active declined with season, so that nests failing in March and April were active significantly longer than those failing in June or July ($r = -0.4$, $P < 0.01$, $N = 64$). The average time before a nest failed (t_f) was 11.67 days.

The probability of nesting success was low (0.2) in 1980. Nesting success was lower during the incubation period (0.368) than during the nestling period (0.571), although the differences in daily success rates between incubation and nestling phases were not significant for either whole nests (Johnson's statistic = 1.088, $P = 0.28$) or partial losses alone (Johnson's statistic = 1.414, $P = 0.16$).

Studies of 10 banded females (Fig. 3) showed that Abert's Towhees built numerous replacement nests and raised at least two broods when possible. The maximum number of clutches, laid by two females, was six (each laid five replacement clutches). Females that did not succeed in fledging offspring extended their breeding season into July. Thus, the length of the reproductive cycle was, in part, dependent on breeding success.

A direct estimate of the number of nesting attempts gave a value of 3.79 nests/female in 1980 ($N = 8$, two females were excluded because of incomplete data). This is a rough estimate, however, because sample size was limited and females were difficult to follow within their large territories (mean territory size was 1.22 ha, $N = 7$, measured in 1979). Replacement nests that were active for only a few days may have been missed.

An expected number of nesting attempts was estimated with Ricklefs' (1973) indirect method. The length of an average nesting attempt by towhees was 31.73 days. Average season length (Ricklefs 1973) was equal to 124.65 days. The number of nesting attempts was equal to $124.65/31.73 + 1 = 4.93$. Fecundity, estimated by multiplying average clutch-size by the number of nesting attempts, was 14.05 eggs/female. Annual productivity in 1980

was estimated as the probability of nesting success times fecundity and was 2.8 fledglings/pair or 1.4 fledglings/individual.

Discussion.—Productivity is influenced by both length of season and timing of onset of reproduction. Early breeding and a long breeding season are advantageous in coping with high nesting mortality, but the factors determining these characteristics are complex. By breeding as early as possible, towhees can increase breeding season length. A long breeding season favors productivity by increasing opportunities to renest, especially after failures. Initiation of breeding requires adequate food supply and nesting sites and materials. In this study, Abert's Towhees had a prolonged nesting season of 4.2 months, compared to an average of 2.17 months for eight Arizona passerine species reported in Ricklefs and Bloom (Auk 94:86–96, 1977). Towhees began breeding shortly after a February peak in rainfall. My data are in apparent agreement with Marshall's (1963) contention that the onset of reproduction is associated with rainfall. Early breeding, possibly initiated by rainfall, was facilitated by flexibility of nest-sites and nest materials (Finch, M.S. thesis, Arizona State Univ., Tempe, Arizona, 1981). However, insect biomass along the lower Colorado River is typically much lower in March than later in the season (Cohan et al., USDA For. Serv. Gen. Tech. Rept. WO-12:371–381, 1978; Anderson et al., Am. Nat. 120:340–352, 1982), and I observed one-egg clutches and nestling starvation at this time. Nonetheless, the combined effects of predation and brood parasitism later in the breeding season lead to the greatest probability of nesting success early in the season (Finch 1983). Thus, early breeding appeared to be favored but may be limited by food availability in March.

Another factor affecting annual productivity is the rapidity of nest replacement. In 1980, the time interval between nesting attempts declined as the season progressed. Increase in the rapidity of nest replacement may be: (1) an adaptation to save time before the favorable period for breeding ends; (2) a response to an environmental change (e.g., increased food supply or nesting material); (3) a behavioral adjustment to a physiological change (e.g., hormonal production); or (4) an improvement because of recent practice. More nests can be attempted during the breeding season if the number of days spent in non-nesting pursuits is minimized.

I have shown in this study that nesting success is not the only factor influencing productivity in Abert's Towhees. Towhees can adjust length of breeding season and rapidity of nest replacement in order to maximize the number of nesting attempts per season. In conclusion, by maximizing the time available for renesting, towhees to some extent can regulate their annual productivity despite low nesting success.

Acknowledgments.—I thank R. D. Ohmart, A. T. Smith, and R. C. Szaro for advice during this study and S. H. Anderson, D. F. Johnston, R. J. Raitt, R. T. Reynolds, J. Rice, and D. Schluter for critical review of the manuscript.—Deborah M. Finch, *Rocky Mountain Forest and Range Experiment Station, 222 South 22nd St., Laramie, Wyoming 82070.* *Accepted 22 Feb. 1984.*

Wilson Bull., 96(4), 1984, pp. 705–708

Aspects of nestling growth in Abert's Towhee.—Among factors selecting for rapid growth rates in avian young are those that cause mortality of whole broods (e.g., predation, weather) (Ricklefs, Ecology 50:1031–1039, 1969). Abert's Towhee (*Pipilo aberti*) endures a high rate of nesting mortality caused by predation and brood parasitism (Finch, Condor 83:389, 1981; Condor 85:355–359, 1983). Predation is the principle factor causing loss of whole broods. Nesting mortality may have an important role in the development of life history traits (e.g.,

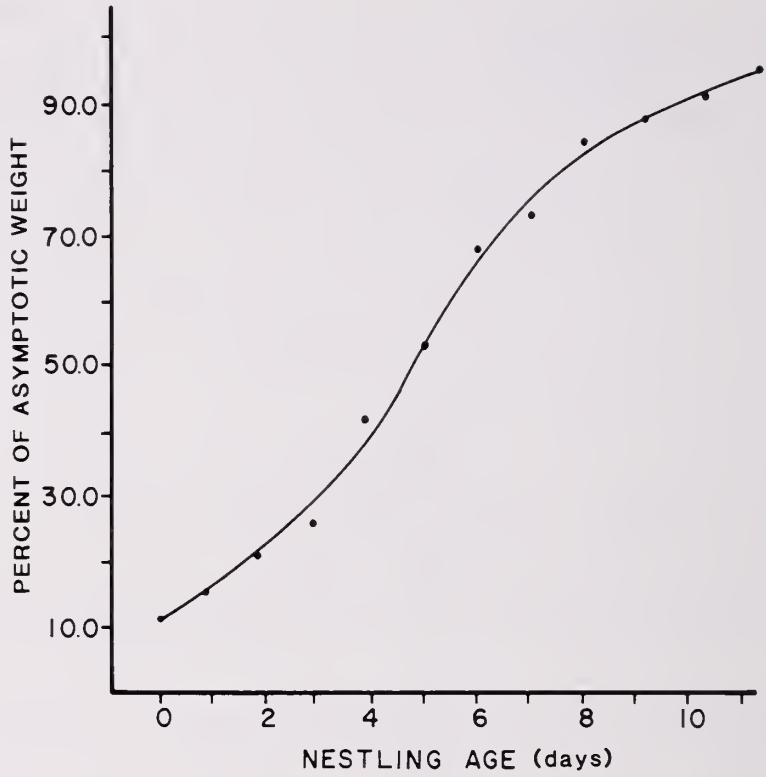

FIG. 1. Growth curve of Abert's Towhee nestling calculated from Ricklefs' (1967) logistic model. Growth equation = $32.8/1 + e^{-0.476(t-4.7)}$. Hatching day = 0.

nestling growth, clutch-size, number of broods/season) in Abert's Towhee, yet little is known about these traits (but see Finch, Wilson Bull. 96:703–707, 1984). In this study, I describe growth rate of nestling Abert's Towhees and discuss its possible adaptive significance. I studied nestlings of Abert's Towhee in honey mesquite (*Prosopis glandulosa*) habitat of the lower Colorado River Valley 10 km N of Ehrenberg, Yuma Co., Arizona.

Methods.—I estimated nestling growth rate by means of Ricklefs' (Ecology 48:978–983, 1967) logistic model, in which the weight of the bird in grams (W) at a certain age in days from hatching (t) is equal to $A/1 + e^{-K(t - t_o)}$, where A = asymptote of the growth curve, K = the growth rate constant $4(dW_i/dt)$, and t_o = age at the point of inflection of the growth curve. Weights of nestlings from seven broods were measured with an Ohaus scale accurate to 0.01 g, and wing chord and tarsus length were measured with calipers. Because nestling mortality occurred in some broods, a growth curve was estimated from composite data for each day of the nestling stage. The growth index (G) (Ricklefs 1967; Auk 96:16–30, 1979a) allowed comparison of tarsus and feather growth and was calculated by the formula: $G = 0.445 \ln [W/(1 - W)]$.

Results.—The hatching weight of Abert's Towhee was 3.63 ± 0.075 g (N = 8 clutches,

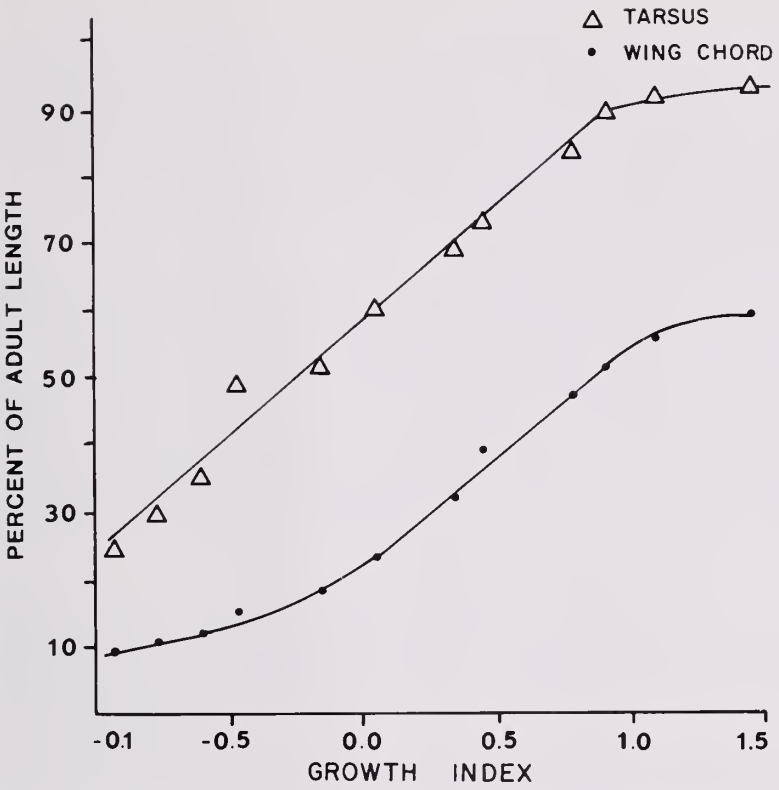

FIG. 2. Development of wing chord and tarsus as percentages of adult length plotted against the growth index (G) = 0.445 ln [W/(1−W)], where W = nestling weight at a given age.

13 eggs) and was 7.8% of adult weight. Towhees fledged at a mean asymptotic weight of 32.8 g. Adults weighed 46.8 g (N = 13, sexes combined) so that the ratio (R) of asymptotic weight to adult weight was estimated to be 32.8/46.8 = 0.70. The instantaneous growth constant (K) was equal to four times the slope (0.122 of the logistic conversion curve) and was estimated to be 0.476. The growth curve of Abert's Towhee was approximated by the logistic equation having the form: $32.8/1 + e^{-0.476(t-4.7)}$. Nestling growth measured as a percentage of the asymptotic weight and plotted against nestling age in days described a sigmoid curve (Fig. 1). The curve did not level out at the end of the nestling period indicating that towhees were still growing rapidly at the time of fledging.

Flight did not appear in Abert's Towhees until a week after fledging, but young could run at 10 days of age. When plotted as a function of the growth index, wing chord can be seen to remain less developed than the tarsus during the nestling period (Fig. 2). Tarsus length was 93% of adult tarsus length at fledging, whereas wing chord at fledging was only 59% of adult wing chord.

Discussion.—The length of the nestling period is related to growth rate. The growth rate

of a species is determined within narrow limits by adult body size and mode of development (Ricklefs, Ibis 115:177–209, 1973). Hence, variation in growth rate among species is not directly explained by energy requirements or rate of nestling mortality. Adult Abert's Towhees weigh three times as much as another desert emberizine, the Rufous-winged Sparrow (*Aimophila carpalis*). Adult Rufous-winged Sparrows weigh 15.3 g and their nestlings have high growth rates (K = 0.57, Austin and Ricklefs, Condor 79:37–50, 1977). When the growth rate (0.476) of Abert's Towhee is scaled to an adult body weight of 15.3 g by use of the relationship $K_2 = K_1 (W_2/W_1)^b$ and $b = -0.26$ (Ricklefs 1979), K for the towhee becomes 0.637. Thus, adult body weight partially explains differences in growth rates of Abert's Towhees and Rufous-winged Sparrows.

Abert's Towhee is a large emberizine with a short nestling period relative to adult body size. Abert's Towhees have completed only about 70% of their growth when they leave the nest, and parents continue feeding them long after fledging. Sparrows, in general, are still growing and accumulating energy in their tissues at fledging (Austin and Ricklefs 1977).

The ratio of fledgling weight to adult weight (R) of Abert's Towhees is somewhat lower than the R value for smaller species of *Pipilo* such as the Rufous-sided Towhee (*P. erythrophthalamus*) in Pennsylvania (Ricklefs, Ibis 110:419–451, 1968). Compared with the R values for other temperate emberizine species (Ricklefs 1968), offspring of the genus *Pipilo* fledge at light weights relative to adults. A regression of R against adult weight for emberizines ($r = -0.54$, N = 18, data from Ricklefs 1968, Austin and Ricklefs 1977, this study) indicated that R is inversely related to adult weight. Because the regression is significant ($P < 0.05$), low R values in large emberizines like towhees are not unexpected.

The difference in maturity at fledging between the wing chord and the tarsus may be dependent on the importance of the structure after the nestling leaves the nest (Ricklefs 1968). An adult Abert's Towhee spends much of its foraging time scratching on the ground with its feet (Marshall, Condor 62:49–64, 1960; Finch, Auk, 101:473–486, 1984). At fledging, its legs must be well-developed for the bird to learn the locomotory skills of feeding. On the other hand, an aerial forager like a swallow (*Hirundo* sp.) depends primarily on its wings for hunting, and it leaves the nest fully grown (Ricklefs 1968). In addition, towhee young tend to run from danger rather than fly, and thus, escape may be an important reason for advanced tarsal development.

Nestling mortality may be the major selective factor driving growth rate to its physiological maximum (Ricklefs 1969). The rate of nestling mortality is high in Abert's Towhee (Finch, Auk 99:719–724, 1982; 1983), and therefore it is adaptive to complete the nest cycle as quickly as possible, particularly because the probability of predation increases over time. The short nestling period of Abert's Towhees may be an adaptive compromise between high nestling mortality and internal developmental constraints (e.g., the slowest-growing-tissue hypothesis (see review, Ricklefs, Biol. Rev. 54:269–290, 1979b). Cryptic ground coloration and early ground mobility aid a fledgling's chance for success.

In conclusion, mobility in the face of predators and, hence, maturity of locomotory function, may ultimately set the limit to length of the nestling period. Success of Abert's Towhee in a difficult environment may be partially explained by its rapid development and short nest period.

Acknowledgments.—I thank R. D. Ohmart, A. T. Smith, and R. C. Szaro for their technical advice, D. R. Patton for his encouragement, and D. F. Johnston and R. J. Raitt for commenting on an earlier draft of the manuscript.—Deborah M. Finch, *Rocky Mountain Forest and Range Experiment Station, 222 South 22nd St., Laramie, Wyoming 82070.* *Accepted 22 Feb. 1984.*

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Cooperative breeding in the Bobolink.—Helpers at the nest (Skutch, Auk 52:257–273, 1935) or auxiliaries (Parry, Emu 73:81–100, 1973) have been reported in over 150 species of birds (Skutch, Condor 63:198–226, 1961; Harrison, Emu 69:30–40, 1965; Fry, Ibis 114: 1–14, 1972; Brown, Am. Zool. 14:63–80, 1974; and Ann. Rev. Ecol. Syst. 9:123–155, 1978; Rowley, pp. 657–666 *in* Proc. XVI Int. Ornithol. Congr., Canberra, Australia, 1976; Grimes, Ostrich 47:1–15, 1976; Woolfenden, pp. 674–684 *in* Proc. XVI Int. Ornithol. Congr., Canberra, Australia, 1976; Zahavi, pp. 685–693 *in* Proc. XVI Int. Ornithol. Congr., Canberra, Australia, 1976; Orians et al., pp. 137–151 *in* Evolutionary Ecology, B. Stonehouse and C. M. Perrins, eds., University Park Press, Baltimore, 1977; Emlen, pp. 245–281 *in* Behavioral Ecology, J. R. Krebs and Davies, eds., Sinauer, Sunderland, Massachusetts, 1978; and Am. Nat. 119:29–53, 1982). Most species of cooperative breeders are tropical or sub-tropical in distribution and are characterized as sedentary, have low fecundity, deferred maturation, long life span, and low dispersal (Brown 1974). As a result there is a limited chance for a young bird to attain a suitable territory or mates (Brown 1978). Helping has also been reported for a few long-distance migratory species such as the Barn Swallow (*Hirundo rustica*) (Forbush, Birds of Massachusetts and Other New England States, Mass. Dept. Agric., Boston, Massachusetts, 1929; Skutch 1961; Myers and Waller, Auk 94:596, 1977) and the Chimney Swift (*Chaetura pelagica*) (Dexter, Wilson Bull. 64:133–139, 1953; Ohio J. Sci. 69:193–213, 1969).

The Bobolink (*Dolichonyx oryzivorus*) is a long distance migratory species which breeds in North America and is single-brooded (Martin, Ph.D. diss., Oregon State Univ., Corvallis, Oregon, 1971; Wittenberger, Condor 80:355–371, 1978; Johnsgard, Birds of the Great Plains, Univ. Nebraska, Lincoln, Nebraska, 1979; pers. obs.). Individuals faithfully return to their breeding areas (Martin, Am. Zool. 14:109–119, 1974; Wittenberger 1978), but helpers have not been previously reported.

During casual observations of 14 nests 10 km southeast of Geneseo, Livingston Co., New York during June 1981 and 1982 we observed helpers, i.e., more adults than the mated pair, attending three of the nests. Observations at the study area were made daily from 1–20 June 1981, and 16–17 June 1982. Most of our observations were from 07:30–14:00, but occasionally extended later. One to 4 h of observation were made at each of the 14 nests. Three h of observation (over 2 days) were made at the first nest below, and 2 h each at the other two nests. At the first nest (11 June 1981), which contained five 5-day-old young, at least two females and one male were observed carrying food to the young. The birds were not color-marked, but we each simultaneously followed a different female and thus determined that two females were involved. We did not follow the male, but based on his habitual use of the same perches and his behavior, we concluded that probably only one male was present. During our observations, each female made about four–five feeding trips/h and the male made 3–4 trips. These rates are similar to those reported by Martin (1974). At the second (16 June 1981) nest, in a field adjacent to the first field, one female and three unbanded males were observed attending five 9-day-old young simultaneously. While we were watching, the female and two of the males carried food to the nest. The third male did not carry food to the nest. Because the males were unmarked, we could not determine their feeding rate. The female made about four trips/h while we were watching. The third (17 June 1982) nest had at least two unbanded adult females and one adult male in attendance and carrying food to the four 10-day-old young. The number of females was again determined by each of us simultaneously following a different female which attended the nest. The females made four–five feeding trips/h and the male made two trips.

The frequency of helpers in our study was 0.21 (3 of 14 nests). Because our observations were not continuous over long periods, it is possible that we did not detect other instances of helping and thus underestimated its frequency.

What would have been the eventual fate of the nests is not known because we took the young and hand-reared them for orientation experiments. The relationships, if any, of the individuals attending the nests is, of course, unknown.

Without knowing the relationship of the individuals involved, it is difficult to ascertain the advantage to the helpers. One explanation is that the individuals outside the breeding pair had recently suffered the loss of their nest and were still physiologically motivated to feed young. This would require the intrusion into an established territory by an outsider, but Wittenberger (pers. comm.) found that after the young hatch, territorial behavior and territory defense essentially cease. Wittenberger (pers. comm.) has also observed adults other than the parents visit a nest. Because these individuals never carried food to the nest, he interpreted the behavior as "information gathering" by the non-parents. All the birds we observed, except one male at the second nest, carried food to the nest. Although we were concealed about 10–15 m from the nest, we could not determine whether the adults actually gave the food to the young or ate it themselves while standing beside the nest.

This is one of very few records of a trans-equatorial migrant which has adult (and presumably sexually mature) helpers at the nest. For other migratory species with cooperative breeding, the helpers are usually young of the year. Because the Bobolinks are long lived (Martin, Bird-Banding 44:47–58, 1973) and return to their previous breeding locations regularly (Martin 1974; Wittenberger 1978 and Ecology 61:140–150, 1980), it is conceivable that the helpers were related to the birds being helped. This possibility is so intriguing from a theoretical aspect, based on kin selection theory (Hamilton, J. Theoret. Biol. 7:1–52, 1964), that we are reporting these observations with the hope that they will stimulate further studies with marked birds to investigate the relationship between the helpers and the individuals they help.

Acknowledgments.—Financial assistance was provided in part by a grant from NSF (BNS 81-02794) to R. C. B. Jerram L. Brown, S. T. Emlen, J. F. Wittenberger, and G. E. Woolfenden provided helpful comments on earlier drafts.—Robert C. Beason and Leslie L. Trout, *Biology Dept., State Univ. New York, Geneseo, New York 14454.* *Accepted 15 Mar. 1984.*

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Cooperative foraging and courtship feeding in the Laughing Gull.—Cooperative foraging (two or more individuals assisting each other in obtaining prey) has apparently not been previously reported in any gull species. I made the following observations of cooperative courtship feeding in Laughing Gulls (*Larus atricilla*) while conducting a study on shorebird foraging at Little Beach Island, Brigantine National Wildlife Refuge in Ocean County, New Jersey. During May and early June Laughing Gulls in New Jersey feed on horseshoe crab (*Limulus polythemus*) eggs, buried on sandy beaches (Wander and Dunne, Records of New Jersey Birds 7:59–64, 1981). They uncover the eggs by treading with both feet at the water's edge and then scooping up the eggs which float to the surface. The approach of a conspecific within 15–40 cm usually elicited aggressive acts such as long calls, jabbing with the gape exposed, and pecking with the bill closed.

On three occasions, 24 May 1981, 30 May 1981, and 25 May 1982, I observed two Laughing Gulls feeding on *L. polythemus* eggs, with their shoulders often touching and no apparent aggression. As none of these birds were individually marked, it is possible, but

not likely, that I observed the same individuals on the three occasions. I was able to distinguish between the two birds by continuously watching the pair and noting the location of one bird relative to the other. For these three observations the birds presumed to be males are identified as gull A and the birds presumed to be females are identified as gull B. On each of the three occasions one gull, A, was treading and the other gull, B, was scooping the eggs out of the water. I did not observe gull A eating any eggs. This continued for 3–4 min until the two gulls walked up on the beach side by side with gull B long calling and head tossing. On 25 May 1982, both gulls long called and head tossed as they walked up the beach; gull A subsequently chased gull B. During all three observations gull B begged and pecked at gull A's bill. On 30 May 1981 and 25 May 1982 gull A regurgitated *L. polythemus* eggs and both gulls ate the eggs. On each of the three occasions gull A mounted gull B, gull B moved its tail to one side, and gull A gave the "gackering call" while copulating.

Courtship feeding is a basic part of pair formation among gulls (Tinbergen, The Herring Gull's World, Collins, London, England, 1953; Moynihan, Behaviour 13:112–130, 1958). Regurgitation is the most common method of courtship feeding in Laughing Gulls, although males have also been observed presenting a whole fish to the female (Noble and Worm, Ann. N.Y. Acad. Sci. 45:179–220, 1943). These three cases of a male uncovering *L. polythemus* eggs and allowing a female to eat the eggs may be a form of courtship feeding. These episodes took place several minutes before the male mounted the female and on 24 May 1981 there was no regurgitation prior to copulation. At Brigantine most first eggs are laid by female Laughing Gulls on 25, 26, or 27 May, so these observations took place during the egg-laying period (Montevecchi et al., Ibis 121:337–344, 1979).

Cooperative foraging is a rare occurrence in birds; one example is White Pelicans (*Pelecanus erythrorhynchus*) cooperatively driving fish into shallow water (Welty, The Life of Birds, Saunders, Philadelphia, Pennsylvania, 1982). Foraging for *L. polythemus* eggs requires that an individual perform two activities: treading and then scooping up the eggs as they float to the surface. It is even more unusual for foraging activities to be uncoupled such that two individuals can forage cooperatively by each performing one activity. Another apparent example of such cooperative foraging is a report of team hunting and food sharing by two Parasitic Jaegers (*Stercorarius parasiticus*) feeding on a Pectoral Sandpiper (*Calidris melanotos*) (Pruett-Jones, Wilson Bull. 92:525–527, 1980).

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Pairing behavior and pair dissolution by Ring-billed Gulls during the post-breeding period.—The pairing behavior of gulls has most commonly been described in the pre-egg-laying period of the reproductive cycle (e.g., Moynihan, Behaviour 13:112–130, 1958). Pairing behaviors are much less frequent during incubation and are rare during chick-rearing (Fetterolf, unpubl.). Herein, I report observations of pairing behavior and pair dissolution by Ring-billed Gulls (*Larus delawarensis*) which occurred during the post-breeding period immediately after these birds had cared for young. I discuss the relationship among post-breeding pairing behavior, pair dissolution, and breeding success and examine hypotheses which may explain the occurrence of such behavior.

Study areas and methods.—I observed post-breeding pairing behavior by Ring-billed Gulls in June and July 1976–1978 on Mugg's Island, Toronto, Ontario, Canada (for description of the site see Fetterolf, Can. J. Zool. 57:1190–1195, 1979) and in June and July 1980–1983 on the Eastern Headland, Toronto Outer Harbour, Toronto (for site description see Blokpoel and Fetterolf, Bird-Banding 49:59–65, 1978). I quantified these events on Mugg's Island in 1978 and on the Eastern Headland in 1983 by noting the number of days on which a pair exhibited pairing behaviors.

All nests had been individually marked during visits every second day during egg-laying and these pairs were observed during other research for approximately 4–6 h daily (05:00–11:00 or 15:00–21:00; for details on methodology see Fetterolf, Anim. Behav. 31:1018–1028, 1983). I determined the number of eggs hatched and the number of chicks fledged and conducted behavioral observations from blinds situated 3–10 m from the study plots (Fetterolf 1983).

On Mugg's Island, I observed 126 pairs for approximately 200 h while taking 1-min samples of behavior after the first egg hatched and until all but two chicks reached fledging age of 35 days. Two pairs that engaged in post-breeding pairing behavior lost all their chicks before fledging whereas the other pairs that performed these behaviors had fledged young that had left the natal territory. On the Eastern Headland I watched 29 pairs for about 180 h while taking 5-min samples of behavior after egg-hatching. These observations continued only until the oldest chick was 35 days of age. The post-breeding pairing behavior I report from the Eastern Headland was observed only for pairs whose entire broods had died. Because of these differences between colonies, I treat each separately.

Gulls on Mugg's Island were not individually marked but I am confident that I correctly identified about 80% of the birds each time I saw them by using the pattern of white spots on the primary feathers and distinctive characteristics such as metal leg bands, bowed-legs, and unusual bill or leg coloration. I had observed these gulls for about 400 h before these data were collected (including the pre-egg-laying and incubation periods). Behavioral clues also strongly suggested that the birds I observed pairing were those that had nested previously on the territories where post-breeding pairing behavior was observed. First, pairing birds "choked" at the nest-site (see below) even though the nest had long been obliterated. Second, pairing birds defended the same territorial boundaries as the pairs that nested on the territory. Third, fledged young occasionally alighted on the territory and were greeted amicably and sometimes fed by the adults. Finally, non-territorial birds behaved very differently than breeding, territorial gulls. The former were "anxious" and exhibited sleeked plumage, erect posture with neck extended, and a rapid walking pace as if "tip-toeing."

On the Eastern Headland in 1983, 48 (83%) of 58 incubating gulls were individually marked with printers' ink of different colors (A. B. Dick Company). Sponges were soaked in dye and placed at nest rims or the birds were sprayed with a plant mister. I identified unmarked birds using the plumage, physical, and behavioral characteristics listed above.

I subjectively sexed gulls using the larger body size and more robust bill of the male as criteria (Ryder, Bird-Banding 49:218–222, 1975). This method has proven to be accurate for 97.5% of the birds (Fetterolf, Wilson Bull. 96:12–19, 1984).

Pairing behaviors which occur before egg-laying are described by Moynihan (1958). For the purposes of this study, I define two stages of pairing behavior. During the pre-egg-laying period, stage 1 (hereafter aggressive pairing) occurs early in the pairing process and is characterized by males "charging" at females on the territory. Later in pair formation in the pre-egg-laying period, stage 2 (hereafter non-aggressive pairing) occurs and lacks male charging at the "mate." Stage 2 is further characterized by bouts of "head-tossing" which sometimes end in "courtship feeding" or "copulation" and by frequent carrying of nest material, "choking" and "scraping" at the prospective nest-site. I observed aggressive and

non-aggressive pairing behavior during the post-breeding period but with only incomplete copulatory sequences.

Results.—*Mugg's Island.*—Forty-eight (38%) of 126 pairs exhibited post-breeding pairing behavior on at least 1 day. Twenty-two (46%) of these 48 pairs had at least one egg fail to hatch and 14 (29%) had at least one chick die before fledging. Thirty (39%) out of the 78 pairs that did not engage in post-breeding pairing behavior had at least one egg fail to hatch and 10 (13%) had at least one chick perish before fledging. The failure of at least one egg to hatch in a nest did not differ between pairs that engaged in pairing and those that did not ($\chi^2 = 0.67$, df = 1, $P > 0.05$). However, pairs that performed pairing displays lost at least one chick before fledging more often than pairs that did not engage in these displays ($\chi^2 = 5.50$, df = 1, $P < 0.05$).

Fourteen (29%) of the 48 pairs that engaged in post-breeding pairing behavior exhibited the aggressive form. Of these 14 pairs that performed aggressive pairing behavior, five males apparently drove off their resident mates and formed pairbonds with new females. I was certain of the identification of both members of the original pair in only two of these five cases. By pairbond I mean that aggression between the new "mates" became rare—the birds usually arrived and departed together, and they both defended the territory. Males began the process of pair dissolution by choking at the nest with the resident mate and then repeatedly chasing her from the territory. Eventually, the resident mate failed to return for several days even though the male "advertised" by "long calling". However, other females did land on the territory (often several at once). Males then went through the entire pair formation process with a new female.

Eastern Headland.—On the Eastern Headland, 14 pairs (48%) of 29 lost their entire brood at least 5 days before observations ceased compared with three (2%) of 126 pairs that failed completely on Muggs's Island ($\chi^2 = 46.08$, df = 1, $P < 0.005$). Ten (71%) of these 14 pairs that failed completely on the Eastern Headland engaged in aggressive post-breeding pairing behavior. Of the pairs that performed pairing behavior, proportionately more pairs were involved in the more aggressive form of pairing on the Eastern Headland than on Mugg's Island ($\chi^2 = 6.49$, df = 1, $P < 0.05$).

In 8 of the 10 pairs that engaged in aggressive pairing behavior on the Eastern Headland, the resident female mates persisted in returning to the territory despite violent attacks by their mates. In the other two pairs that exhibited aggressive post-breeding pairing behavior, the two marked females failed to return to their mates for several days. The males from these two pairs were engaged in aggressive pairing behavior with unmarked females when observations were discontinued.

Discussion.—My observations of marked individuals on the Eastern Headland showed that gulls that performed post-breeding pairing behavior were birds which had nested. Mortality of chicks may have precipitated aggressive pairing behavior and pair dissolution. For species that form long-term pair bonds "divorce" (here called pair dissolution) is defined as forming a pair with an individual other than the mate of the previous (in this study, current) breeding season when the previous mate is known to be alive (Coulson, pp. 424–433 *in* Proc. XV Int. Ornithol. Congr., The Hague, Netherlands, 1972). Black-legged Kittiwakes (*Rissa tridactyla*) (Coulson 1972), Red-billed Gulls (*Larus novaehollandiae scopulinus*) (Mills, J. Anim. Ecol. 42:147–162, 1973), and Northern Fulmars (*Fulmarus glacialis*) (Ollason and Dunnet, J. Anim. Ecol. 47:961–976, 1978) had poorer breeding success when individuals lost their mates due to divorce or death than when individuals retained their mates. In kittiwakes (Coulson 1972) and fulmars (Ollason and Dunnet 1978), individuals that divorced had higher breeding success than individuals that changed mates because the previous partner died. Coulson (1972) reported that divorce was more common for pairs that failed completely than for pairs that reared at least one young. All pairs that engaged

in post-breeding pairing behavior on the Eastern Headland failed completely whereas nearly all gulls on Mugg's Island had fledged at least one chick so it is notable that aggressive post-breeding pairing behavior was more frequent at the former site than at the latter.

Coulson (1972) suggested that divorce was caused by asynchronous arrival of previous mates at the breeding colony in the year following the premature breakup of the pair due to nesting failure. He thus implied that a delay in pair formation and perhaps the additional time required to pair with a new individual were responsible for lower breeding success. Such an explanation does not account for the lower success of widowed than divorced individuals. Mills (1973) suggested that birds that changed mates for either reason began egg-laying later and laid smaller clutches because they had less foraging time resulting from more time spent pairing than gulls that did not change mates. One way for birds to overcome some of the disadvantage associated with changing breeding partners would be to form new pairs before the upcoming breeding season. I do not know whether the pair dissolutions I observed lasted to the next breeding season, but some Ring-billed Gulls may have ameliorated the disadvantages by obtaining a new mate immediately after breeding. In contrast, if widowed birds discover the loss of their previous mate only when they return to the breeding colony, breeding may be delayed and therefore comparatively less successful than for other pairs. Then some of the difference in breeding success between widowed and divorced individuals in kittiwakes and fulmars may be explained by pair dissolution and pairing with a new mate immediately after breeding.

The non-aggressive post-breeding pairing behavior I observed may strengthen pairbonds and the bond to the site thus facilitating reacquisition of the previous mate in the following breeding season. Returning to the same site in subsequent years is thought to play a major role in the reformation of pairs of colonial nesting birds (Hunt, pp. 113–151 *in* Behavior of Marine Animals. Vol. 4: Marine Birds, J. Burger, B. L. Olla and H. E. Winn, eds., Plenum, New York, New York, 1980).

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Consequences of mate loss to incubating Ring-billed and California gulls.—Recently, attention has been focused on the strategies that gulls, which have lost their mates, may employ to raise their offspring. It had been assumed that the only option for these gulls was to raise the young themselves. However, Pierotti (Am. Nat. 115:290–300, 1981) observed male Western Gulls (*Larus occidentalis*), which had lost their mates during the incubation period, recruiting new female mates who helped them raise their young. Pierotti (1981) argued that this seemingly altruistic behavior on the part of the female helpers would benefit them if breeding males were in short supply and if the female helpers were able to pair with these males in subsequent years.

Likewise a widowed female may be able to recruit a male to form a heterosexual pair or another female to form a female-female pair (Ryder, Proc. Colonial Waterbird Group

2:138–145, 1978). In the latter case, the second female could lay her eggs in the mutual nest, resulting in the supernormal clutch found in many nests attended by female-female pairs. Hence, each female would have a chance to raise her own offspring. Alternatively, female-female pairs may form at the beginning of the breeding season in the same manner as a heterosexual pair (Hunt and Hunt, Science 196:1466–1467, 1977).

Unfortunately, there are insufficient data to determine which mechanism accounts for most female-female pairings. Some female-female pairs show mate fidelity from one year to the next (Hunt and Hunt 1977; Kovacs and Ryder, Auk 98:625–627, 1981); consequently, once established, female-female pairs may re-mate in subsequent years in the same manner as heterosexual pairs, but this leaves unanswered the question of how these pairs are initially formed.

I had an opportunity in 1981 to study the consequences of mate loss in Ring-billed Gulls (*Larus delawarensis*) and California Gulls (*L. californicus*) when someone shot several color-banded birds early in the incubation period in the Potholes Reservoir colony near Moses Lake, Grant Co., Washington. As the nest-sites of these birds were known, I was able to observe the effect of this loss on the mate's behavior and breeding success. Additional subjects were added when I trapped and held their mates in captivity for a 2-week period before releasing the mates unharmed.

Among California Gulls, I identified five females and five males which had lost their mates early in the incubation period. On the first day after losing their mates, all of them left their territories for part of the day. This absence apparently resulted in egg predation because, by the following day, four of the females and three of the males had lost their clutches. One female retained her clutch for 1 week, possibly because her nest was located in heavy vegetation and was inconspicuous. After 2 weeks, only one of her three eggs remained and she had abandoned the nest. The two males still caring for their nests after the second day also were unsuccessful; one clutch was destroyed and the other was abandoned during the first week.

I also watched five female and three male Ring-billed Gulls which had lost their mates early in the incubation period. On the first day after losing their mates, three of the females and two of the males began leaving their territories, and within 24 h one male and one female had lost their clutches. By the end of the second day, all clutches were destroyed except for one cared for by a female and one by a male. The eggs in these two nests, however, were also destroyed or the nest abandoned within 1 week.

None of the Ring-billed or California gulls that lost mates was observed courting other birds. When other gulls landed on their territories, the birds drove them away. I did not observe any of these subjects setting up new territories elsewhere or renesting with new mates. Of course, this possibility cannot be excluded because some renesters could have escaped detection during my searches.

These observations contrast with those Pierotti (1981) made for male Western Gulls. All five males he observed recruited a female nest helper within 2 days. Within a similar period, most of the Ring-billed and California gulls which I watched had already lost their clutches. Possibly, this difference occurred because unattended eggs are more likely to be destroyed by neighboring gulls in Ring-billed and California gull colonies due to their smaller territories and nearness to neighbors. Additionally, Western Gull territories may be large enough for an unmated female to remain on the territory of an incubating, widowed male without provoking an attack. Thus, acceptance of a female helper could be accomplished gradually.

In this study, none of the female Ring-billed and California gulls which lost her mate attracted another female and formed a female-female pair. Hence, these results fail to support the hypothesis that most female-female pairings occur when a female loses her mate during the incubation period. I did not ascertain whether female-female pairings could form

when a female is widowed after being fertilized but before beginning to incubate. Nonetheless, given the short time involved, it is likely that too few females find themselves in that predicament to account for most of the female-female pairs.

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Intra- and extrapair copulatory behavior of American Crows.—The copulatory behavior of American Crows (*Corvus brachyrhynchos*) has not been described. The present observations on intrapair copulations (N = 28) and extrapair copulatory behavior were made at the Hendrie Ranch, 24 km S, Lake Placid, Highlands Co., Florida, January–April 1982, 1983, and 1984. The crows at the ranch were relatively tame as described earlier (Kilham, in press). Birds on nests, 6–8 m above ground, were viewed at distances of 10–20 m without the use of blinds.

Identification of sexes of breeding pairs.—My observations are based on two groups (7–9 crows each) of cooperatively breeding crows occupying territories with a common boundary. During the period of greatest copulatory activity, i.e., between the end of nest-building and the third day of incubation, the behavior of the sexes of breeding pairs were clearly distinguishable. The males, the dominant members of groups, devoted much time (unpubl.) to driving away or attempting to drive away some of the adult auxiliaries as well as mate-guarding, in which they either watched the nest when the female was on it or followed her closely wherever she flew. The males frequently held an upright stance and did more wing-tail flicking and "cawing" than other members of their group. One male, identified sexually at times of copulations, had a missing right rectrix in 3 successive years. The breeding females, in addition to egg-laying and doing all of the incubating, were distinguishable at times by their never attacking other crows of their own group and, when perched by their mates and elsewhere, in having hunched postures with wings hanging loosely, which gave them a relaxed appearance. One female, identified at times of copulation, had a forked tail due to a breaking off of central rectrices. Criteria distinguishing adult from yearling crows are described by Emlen (Condor 38:99–102, 1936).

Intrapair behavior.—Twenty-eight copulations were observed both on nests and on the ground. A female was giving slow *caw-caw-caws* on her nest on 13 January when her mate came to the rim and mounted. I heard a single *cu-koo*. The male settled, waving his outspread wings which came to hang over the edge of the nest. The female stood up beneath him, her tail vibrating up and down as he worked his tail under hers. On the next day, the second of egg-laying, he again came to the rim, placing a foot on her neck before mounting. This time her body sank low as her head tilted way back. The crows vocalized (bills open) so loudly that they were audible at 250 m. Similar loud cries were heard in 11 of the 28 copulations.

I watched a crow fly over a pasture on 2 February when it abruptly alighted on a female that was crouching in the grass in a pre-copulatory pose. In the copulation that followed, she put her head back. This was 70 m from the nest. I watched the same female feeding in a pasture later when her mate alighted 5 m away in the same pre-copulatory pose that she had exhibited earlier. She flew to him immediately, also taking a pre-copulatory pose. He

then took a piece of debris about 7 cm long in his bill and, still holding it, mounted her and copulated. Of 28 copulations observed, 17 were on nests, nine on the ground, and two on branches. Copulations were estimated to be 4–12 sec in duration. Four copulations noted for one pair extended from the end of nest-building, through an interim period of 2 weeks, to the third day of incubation.

Pre-copulatory display.—In addition to complete copulations, I witnessed 23 unsuccessful ones. Considering both types together (N = 51) a pre-copulatory display was noted in 29, the females performing in each and their mates performing simultaneously in seven. In a usual display, the male, the female, or both, crouched with body horizontal, wings out and drooping, and tail vibrating up and down. The display is also seen, at times, in juveniles begging from parents. Thirteen of 51 instances of copulatory behavior were preceded by the *cu-koo* vocalization and three by the male (N = 2) or the female (N = 1) holding a stick or other object in the bill.

Extrapair copulatory behavior.—The crows at the ranch fell into two groups of cooperative breeders which, in 1983, consisted of a breeding pair plus five to seven adult auxiliaries. These latter, although attacked repeatedly by the breeding males and driven from the vicinity of nests in weeks when copulatory behavior of the pair peaked, still exhibited signs of sexual activity. On 14 January the two members of one pair had nearly finished a copulation when a second male flew to the nest and landed on the back of the female next to the copulating male. Both males flapped their wings. The three crows rose and fell as the female moved underneath. After a few seconds, the males flew, one chasing the other.

Other instances of extrapair activity were seen on the ground. A breeding female was giving nest calls while feeding in a pasture when an auxiliary, a male, first flying to the unattended nest, flew to her and mounted. The breeding male knocked him away almost immediately, then returned three times within 12 min to attempt to copulate. Two other instances of extrapair activity were initiated by a female auxiliary (X). This individual came below the nest where a breeding female was incubating and crouched in a pre-copulatory pose. The breeding male mounted her. At this the incubating female flew down, lowered her head, and pushed X away. Two days later, again within sight of the nest, both X and the breeding male gave pre-copulatory displays followed by his mounting for a few seconds. None of the extrapair attempts appeared to be complete.

Discussion.—Most accounts of promiscuity in birds, as summarized by Gladstone (Am. Nat. 114:545–577, 1979) have been in colonial nesting species. Among 11 copulations witnessed by Wittenberg (Zool. Jb. Syst. 95:16–146, 1968) for the Carrion Crow (*C. corrone*), a non-cooperative breeder, four were by intruding males. In one of these he saw, as I did with *C. brachyrhynchos,* two males mounted on a female simultaneously. All of the copulations witnessed by Wittenberg (1968) were on nests, Gent (Br. Birds 42:242, 1949) being the only reference to one on the ground. Wittenberg (1968) also describes Carrion Crows as giving loud copulation cries. The pre-copulatory display I noted seems to be common to some other *Corvus* species, Gwinner (Z.f. Tierpsychol. 21:657–748, 1964) describing it in both sexes of the Common Raven (*C. corax*).

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Addendum.—Since this note was written, James (J. Field Orn. 54:418–419, 1983) has published one on reverse mounting in the Northwestern Crow (*C. caurinus*). I should report that I witnessed one instance of reverse mounting among 28 copulations noted for American Crows.—LK.

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Nest parasitism by cowbirds on Buff-breasted Flycatchers, with comments on nest-site selection.—The Buff-breasted Flycatcher (*Empidonax fulvifrons*) is a small flycatcher of the Mexican highlands which regularly breeds in limited numbers in the mountains of southeastern Arizona and southwestern New Mexico. Few details of its life history have been published. Nest parasitism by cowbirds has not been reported for this species. In the course of a general life history investigation of this flycatcher, we established that Brown-headed Cowbirds (*Molothrus ater*) and probably Bronzed Cowbirds (*M. aeneus*) parasitize the nest of this species.

On 5 July 1982, Bowers collected a recently abandoned Buff-breasted Flycatcher nest in Garden Canyon, Huachuca Mountains, Cochise Co., Arizona. In the nest were a small, unmarked, off-white flycatcher egg and a larger, heavily spotted Brown-headed Cowbird egg. Both eggs broke when the nest was taken, but identifiable pieces of shell were recovered. The nest and egg fragments are now in the University of Arizona collection (UA 14390).

On 11 June 1982, Bowers watched a female Bronzed Cowbird make two attempts to sit on a Buff-breasted Flycatcher nest in Sawmill Canyon, also in the Huachuca Mountains. The attempts failed due to the location of the nest in the fork of a horizontal branch. The upper branch of the fork passed directly over the top of the nest. The space between the two branches was so small that only a bird as small as a Buff-breasted Flycatcher (about 8 g) could fit on the nest.

We found 29 nests of *E. fulvifrons* in the 4 years of this study. The fate of the contents of six of these nests is unknown. Of the remaining 23 nests, young fledged from 9 unparasitized nests, while no young fledged from 14 other nests. Four unsuccessful nests were not parasitized, one was parasitized and the contents of the remaining nine unsuccessful nests were not seen.

The failed parasitism attempts observed by Bowers suggest that choice of nest-site can affect the reproductive success of a pair of birds in a way not normally considered by researchers. All but 8 of the 29 nests discovered in this study had a branch passing within 5 cm of the top of the nest. Earlier studies of the Buff-breasted Flycatcher also noted the tendency to build under overhangs (Willard, Condor 25:189–194, 1923; Brandt, Arizona and Its Bird Life, Bird Research Foundation, Cleveland, Ohio, 1951). In addition, nesting under overhangs has been described for other small birds such as Calliope Hummingbirds (*Stellula calliope*) (Bent, U.S. Natl. Mus. Bull. 176:420–429, 1940) and Broad-tailed Hummingbirds (*Selasphorus platycercus*) (Calder, Ecology 54:127–134, 1973). Most early reports suggested that the overhang serves simply as a rain umbrella (Bent 1940). Calder (1973), however, emphasized the importance of the overhang as protection at night against loss of radiation heat from the incubating bird. For birds as small as hummingbirds or perhaps this flycatcher, the shelter helps maintain the birds within tolerable energetic limits (Calder 1973; Calder, Natl. Geogr. Soc. Resear. Rept. 13:145–169, 1981). Our observations indicate a third advantage of having a protective structure over the nest. The overhang can physically prevent a nest parasite from reaching the nest of a smaller host species.

Normally, the loss of a few nests to parasitism may not adversely affect the continued existence of the host population as a whole (Mayfield, Am. Birds 31:107–113, 1977). In areas where the host population is small, however, losses due to parasitism can be quite detrimental (Kelly and DeCapita, Wilson Bull. 94:363–365, 1982). In Arizona, Buff-breasted Flycatcher populations are extremely small (18 pairs in 1982, 9 pairs in 1983, this study), while cowbird populations have recently increased (Monson and Phillips, Annotated Checklist of the Birds of Arizona, Univ. Arizona Press, Tucson, Arizona, 1981). Thus, the con-

tinued presence of Buff-breasted Flycatchers in southeastern Arizona could be partially dependent on the relative inaccessibility of their nests due to overhanging structures.

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Sandhill Crane incubates a Canada Goose egg.—I have previously reported on inter- (Littlefield, Wilson Bull. 91:323, 1979) and intraspecific egg dumping (Littlefield, Auk 98: 631, 1981) in Sandhill Crane (*Grus canadensis tabida*) nests. Except in one nest, which contained one Canvasback (*Aythya valisineria*) egg and two crane eggs, none of the dumped eggs was being incubated.

On 23 April 1982, a Sandhill Crane nest was located 72 km SSE of Burns, Harney Co., Oregon, on Malheur National Wildlife Refuge (NWR). Upon discovery, the male crane was incubating a Canada Goose (*Branta canadensis*) egg (84.7 × 56.2 mm). Also present in the nest bowl were traces of goose down. The nest was typical of Sandhill Cranes and had the following measurements: nest diameter—105 cm; bowl diameter—39 cm; bowl depth—6.6 cm; and nest height above water—20.6 cm. Surrounding vegetation and nest composition was hardstem bulrush (*Scirpus acutus*), and the water depth was 17.4 cm. The goose egg appeared fertile and was estimated to have been incubated about 20 days (see Westerskov, J. Wildl. Manage. 14:56–67, 1950). While the nest was being examined the crane pair performed distraction behavior within 6 m of the nest. Upon reexamination on 1 May 1982, the egg had been destroyed by an unknown predator. At this time I removed all nesting material in an effort to locate crane egg shell fragments; however, none was located.

Sandhill Cranes are normally intolerant of close approach to their nests by other avian species (pers. obs.). How incubation of the goose egg began is unknown, but there are at least three possibilities. (1) Perhaps both crane and goose eggs were in the nest, but the crane eggs were removed by a predator, leaving the goose egg. Coyotes (*Canis latrans*) have often been seen on Malheur NWR removing eggs intact before consuming them at upland sites (pers. obs.). (2) The crane eggs were removed by a predator and the Canada Goose deposited her egg before the crane pair returned to the nest; or (3) although unlikely, the cranes took over the nest after the goose laid her first egg. This would account for the few down feathers present in the nest bowl.

There are several records of Canada Goose eggs being deposited in Sandhill Crane nests (Littlefield 1979; W. Radke, pers. comm.); however, I know of no other record of a goose egg being incubated by a Sandhill Crane pair.

I would like to thank B. Ehlers and S. Thompson for commenting on an earlier draft of this note, and G. Archibald and H. Lumsden for their valuable comments. Special thanks also go to D. D. Ehlers for her typing assistance.—CARROLL D. LITTLEFIELD, *U.S. Fish and Wildlife Service, P.O. Box 113, Burns, Oregon 97720.* *Accepted 31 Oct. 1984.*

Wilson Bull., 96(4), 1984, pp. 720–723

Observations on postures and movements of non-breeding American Woodcock.—Apart from descriptions of male courtship displays, there are few reports on the behavior of American Woodcock (*Scolopax minor*). This paper describes postures and movements of non-breeding birds observed in late summer and early spring.

Observations through a night vision scope on crepuscular concentrations of woodcock at logging road puddles were made from June–September of 1972 and 1973 in the Cloquet Forestry Center (CFC) in northeastern Minnesota (Morgenweck, Ph.D. diss., Univ. Minnesota, St. Paul, Minnesota, 1978). Woodcock activities and social interactions were described and quantified. Sex determinations were made if the bird was marked (Morgenweck and Marshall, Bird-Banding 48:224–227, 1977), on the basis of size and/or peenting. Drawings were made from photos taken through the night vision scope. Other observations of a single bird were made during daylight in St. Paul, Minnesota, over 8.75 h on 4 April 1974 and between 29 March and 1 April 1978 (Marshall, Auk 99:191–192, 1982).

Postures.—*Alert.*—At CFC, woodcock usually landed in the road some distance from the puddle and, while standing upright and motionless, appeared watchful (Fig. 1A). The percent of birds that assumed alert posture upon landing and the duration of this posture was not significantly different between dawn and dusk (Table 1).

At intervals during feeding, a St. Paul bird stood motionless, eyes open, with the bill on the breast. The undisturbed bird assumed this posture eight times, ranging from 0.5–9 min in length. Also, gray squirrels (*Sciurus carolinensis*) or cottontails (*Sylvilagus floridanus*) passing nearby elicited this posture on seven occasions for 1–10 min. Demole (Subtilites de la Chasse à la Bécasse, Librarie Des Champs-Elysées, 1964) described this posture by European woodcock (*Scolopax rusticola*) upon arrival at a pool prior to an evening bath.

Stand rest.—Five times, after it had been in the alert position for a few seconds, a St. Paul bird quickly turned its head and tucked the bill under the dorsal feathers with the eyes closed. These postures lasted 3–26 min.

Rest.—On three occasions a St. Paul bird, while on leaf litter under shrubs, fluffed its ventral feathers and lowered its body to the ground with vigorous side-to-side motions that displaced dry leaves. The tail was lifted, but not spread over the back; the bill was placed in the dorsal feathers; and the eyes were closed. These periods lasted 4–9 min.

Tail flare.—At CFC, an interruption (e.g., when an automobile approached or another woodcock flew overhead) often elicited a tail flare response (Fig. 1B) by both sexes (Table 2). We agree with Sheldon (The Book of the American Woodcock, Univ. Massachusetts Press, Amherst, Massachusetts, 1967) that tail flares are elicited by alarm.

Movements.—*Stitching.*—At CFC, woodcock made repeated probes in the sand and mud of the road, the bill rarely inserted more than 1 cm into the substrate (Fig. 1C). There was no evidence of prey capture, and usually the birds only hesitated to jab as they moved toward a puddle. After reaching the puddle, the birds thrust their bills deeply into soft mud.

Birds then walked into puddles until the water was nearly to the belly feathers, hesitated, then made a series of rapid jabs into the substrate with the bill at an angle of 70–80° below the horizontal. After making one to six jabs, usually with the bill remaining in the water, the bird walked a few steps and repeated the process. On other occasions a woodcock would walk in a zig-zag pattern through the puddle, making jabs at the substrate, and lifting its bill clear of the water between jabs. The percent of birds that stitched and the duration of stitching was not significantly different between dawn and dusk (Table 1). Stitching may be a type of displacement activity (Welty, The Life of Birds, W. B. Saunders Co., Philadelphia and London, 1962).

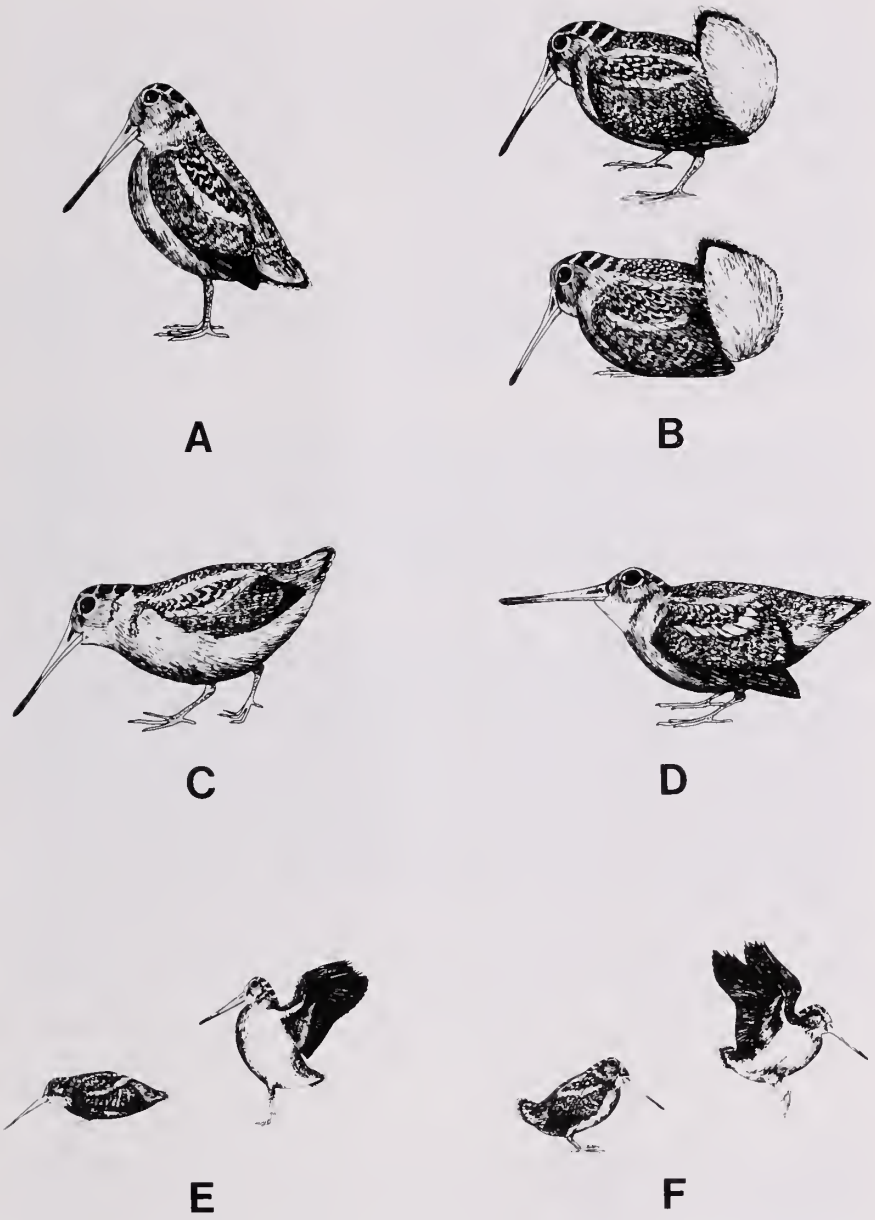

FIG. 1. American Woodcock postures: A. Alert; B. Tail flare; C. Stitching; D. Supplanting chase; E. "V" chase; F. Flutter leap.

TABLE 1

NUMBER AND PERCENT OF AMERICAN WOODCOCK OBSERVED PARTICIPATING AND AVERAGE MIN PER BOUT IN FOUR ACTIVITIES—COMPARING DAWN AND DUSK PERIODS[a]

	% participating dawn/dusk	(N) dawn/dusk	$\bar{x}$/bout dawn/dusk	(N) dawn/dusk
Alert	83/69	36/96	1.5/1.2	13/39
Stitching	85/83	41/118	2.5/3.5	10/40
Bathing	20/71*	35/129	2.5/2.5	2/47
Preening	29/78*	31/74	2.7/3.6	5/40

[a] The number of birds observed participating is greater than the number of birds timed, because it was impossible to time each individual's activity when several birds were present.

* Differences significant ($P < 0.05$).

Feeding.—While rocking on the lawn the 1978 bird both picked up and probed for worms. Also, while under nearby shrubs, the bird turned dead leaves up and to the side with its bill—a few times it used a foot to flick a leaf over, but not in a "scratching" motion. Often the bird reached out quickly to catch something or poked its bill into a rosette of green leaves followed by swallowing. Wilson, (American Ornithology, 6:104–108, Bradford and Inskeep, Philadelphia, Pennsylvania, 1812) noted that "woodcocks will turn over leaves in search of food."

Bathing.—After stitching, the CFC birds walked deeper into the puddle and bathed in a manner described by Slessers (Auk 87:91–99, 1970). More birds bathed at dusk ($\chi^2 = 27.18$, df = 1, $P \leq 0.05$) than at dawn, but there was no difference in the duration of these bouts (Table 1). Similar behavior by the Euorpean woodcock has been reported by Demole (1964).

Preening.—After bathing, CFC woodcock walked to the edge of the puddle and preened, removing feather sheathing and feathers. More birds preened in the evening ($\chi^2 = 20.95$, df = 1, $P \leq 0.05$) than in the morning with no difference in the duration of the bouts (Table 1). Preening peaked in early August which coincides with the peak of molting as reported by Owen and Krohn (Wilson Bull. 85:31–41, 1973).

Supplanting chases.—At CFC, these chases often began after preening (Fig. 1D). A chase

TABLE 2

PERCENT OF WOODCOCK OF KNOWN SEX PARTICIPATING IN FOUR ACTIVITIES

	Male		Female	
	%	N	%	N
Tail flare	21	34	25	20
"V" chases	51	35	54	24
pursuer	89*	18	15	13
pursued	11*		85	
Arc flight	34	35	52	21
Flutter leap	41	34	50	16

* Significant at $P < 0.05$.

occurred when a bird lowered its head and bill to the horizontal and, with wings held slightly away from the body, charged another bird forcing it to run or fly.

"V" chases.—A more common chase resulted when one bird approached another with outspread wings lifted high in a "V" (Fig. 1E). The pursued bird squatted as the pursuer approached to within 0.5 m, but when the pursuer closed to within 25 cm, the pursued bird rose and walked rapidly away. Occasionally this sequence was repeated several times. On other occasions the pursued bird either ran or flew without squatting and, on three occasions the pursuing bird attempted to mount.

The percent of males (51%) and females (54%) participating in "V" chasing was similar. Significantly more males were pursuers (Table 2), and pursued females most often squatted while being approached, whereas pursued males moved away. These encounters may be adolescent sexual displays because Sheldon (1967) described similar behavior preceding copulation and most birds at puddles (79.1%) were hatching year individuals, based on mist net captures. Also, no marked adults participated in the "V" chases. Since Sheldon (1967) reports similar behavior by a male attempting to copulate on a singing ground, these encounters could be adolescent sexual displays.

Arc flight.—At CFC, after alert posture, birds farthest from the puddle often moved closer by flying in a low "arc flight" which was usually less than 15 m long. The percent of males and females performing arc flights was not significantly different (Table 2).

Flutter leap.—At CFC, woodcock often leaped 5–30 cm into the air, fluttered their wings and returned to the same place on the ground (Fig. 1F). Over 91% of those recorded were from the alert position, although flutter leaps also occurred from the squatting or tail flare position. Flutter leaps were performed by 41% of the observed males and 50% of the females (Table 2).

Frequently, pursued woodcock would flutter leap when approached by another bird, and the pursuer would follow suit. There may be a relationship between flutter leaps and precopulatory behavior, as discussed by Sheldon (1967). Flutter leaps, after preening, may have aided in restoring plumage to its proper position. On a few occasions, a bird, stitching near a puddle, would flutter leap. A flutter leap was seen once in St. Paul when a cottontail rushed to within 1 m of the bird.

Acknowledgments.—The facilities of the Cloquet Forestry Station were made available by A. R. Hallgren, and G. W. Gullion assisted in many ways. M. K. Beutlich gave much support and frequent field assistance. N. Kane made the drawings for the figures. Financial support was provided by the Research Program for Migratory Shore and Upland Game Birds, U.S. Fish and Wildlife Service, Contract #14-16-008-52F, through the Minnesota Department of Natural Resources. F. B. McKinney and H. B. Tordoff reviewed the manuscript.—RALPH O. MORGENWECK, *Div. Biological Services, U.S. Fish and Wildlife Service, Fort Collins, Colorado 80526;* AND WILLIAM H. MARSHALL, *7248 Oakmont Dr., Santa Rosa, California 95405.* *Accepted 28 Aug. 1984.*

Wilson Bull., 96(4), 1984, pp. 723–725

Non-territorial adult males and breeding densities of Blue Grouse.—Although it previously was believed that all adult male Blue Grouse (*Dendragapus obscurus*) held territories during the breeding season (Zwickel, J. Wildl. Manage. 36:1141–1152, 1972), recent studies have shown that non-territorial adult (≥2 years of age) males were present in populations in coastal British Columbia (Lewis and Zwickel, Can. J. Zool. 58:1417–1423, 1980; Jamieson and Zwickel, Auk 100:653–657, 1983). Non-territorial males are physiologically able to breed (Hannon et al., Can, J. Zool. 57:1283–1289, 1979), yet in the absence of occupying

territories they are presumed to be non-breeders (Bendell and Elliott, Can. Wildl. Serv. Rept. Ser. 4, 1967; McNicholl, Ph.D. diss., Univ. Alberta, Edmonton, Alberta, 1978). The presence of non-reproductive adults is pertinent to understanding how breeding densities are determined. Here, I present further evidence for the existence of non-territorial adult male Blue Grouse and provide information on their abundance within a natural population on Hardwicke Island, British Columbia (50°28′N, 125°48′W).

I conducted a study concerning aspects of territoriality in male Blue Grouse on a recently logged 95-ha portion of the island from 1980–1982. Almost daily from mid-March or early April through July each year I searched this area for territorial males, these being individuals that were localized on small areas and that were heard hooting (singing) (Bendell and Elliott 1967, McNicholl 1978). Throughout the study period each year these males were resighted repeatedly to determine the exact locations of their territories.

Numbers of territorial males on the study area declined from 28 in 1980 to 25 and 17 in 1981 and 1982, respectively. Of the territorial males that were color-banded (87%), all were adults. Additionally, four marked adults in 1980 and two in 1981 were non-territorial. Three of these were seen between three and eight times and their movements encompassed the territories of three to four other males. The other three were seen only once but were considered non-territorial because they were on the territories of other males during non-migratory periods. At least three of the non-territorial adults from 1980 and one from 1981 survived and took territories in 1981 and 1982, respectively.

I removed original occupants and subsequent replacements from 14 territorial sites in 1982. Six of 10 replacements were adults, all having been banded as yearlings in 1981. These males took territories later in the spring than was typical for males in this population in non-removal years, and they did so only after original occupants had been removed. Therefore, in the absence of my removal experiment I believe that all, or most, of these adults would have remained non-territorial throughout 1982 (see also Lewis and Zwickel 1980). Thus, non-territorial adults were present each year even though the number of territorial males declined.

Because non-territorial males do not hoot they are not found as easily as males that do. Consequently, it is difficult to determine precisely the percentage of young adults that do not take territories. Nonetheless, seven of the eight males that first took territories after my study began had been banded in previous years, and four of these were 3 years of age or older when first taking territories. Additionally, 4 of 10 two-year-old males that were radio-tracked on another area of Hardwicke Island were non-territorial (Jamieson and Zwickel 1983). Thus, evidence from Hardwicke Island corroborates that from Vancouver Island (Lewis and Zwickel, Can. J. Zool. 62:1881–1884, 1982), and suggests that non-territorial adult males are not uncommon within populations of breeding Blue Grouse in coastal British Columbia.

Vacant areas that apparently are suitable for territories are present within the areas where non-territorial males have been found (Lewis and Zwickel 1981). Why these males do not take territories must therefore be explained if we are to understnad how breeding densities of male Blue Grouse are determined. Current evidence suggests that these males remain non-territorial because areas that are available are of low quality (Lewis and Zwickel 1980, 1981). Although some physiologically mature males do not hold territories, this does not seem to affect densities of females or production in the population as neither number of breeding females nor production per female were reduced when numbers of territorial males were greatly lowered in 1982 (Lewis, Can. J. Zool. 62:1556–1560, 1984).

Acknowledgments.—I thank F. C. Zwickel, C. Scharf, and V. Lewin, all of the Department of Zoology, University of Alberta; J. F. Bendell, Faculty of Forestry, University of Toronto;

and S. D. MacDonald, National Museum of Natural Sciences, Ottawa, for comments on the manuscript. Crown Zellerbach of Canada Limited and Bendickson Contractors Limited allowed me to work on Hardwicke Island; while there the hospitality of the Bendickson and Murray families was greatly appreciated. Financial assistance was provided by the Natural Sciences and Engineering Research Council of Canada and the University of Alberta.—
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ORNITHOLOGICAL LITERATURE

AVIAN BIOLOGY, VOL. VII. Edited by Donald S. Farner, James R. King, and Kenneth C. Parkes. Academic Press, Inc., New York and elsewhere, 1983:542 pp., text figures and tables. $69.50.—More than 15 years ago Farner and King sketched plans for a multivolume work to update A. J. Marshall's useful "Biology and Comparative Physiology of Birds," enlisting Parkes as the taxonomic editor. The early volumes had discernible themes: the first on classification, ecology, and evolution; the second primarily morphology and physiology; and the third mainly on endocrinology and sensory apparatus. With volume IV thematic emphasis began to degenerate, the content including some morphology, some physiology, some endocrinology and so on. The present volume VII is about as topically chaotic as one can imagine, with chapters on post-hatching growth, helminth parasites, behavioral ontogeny, ecological energetics, etc. I doubt if anyone is really qualified to review the book adequately throughout; certainly I am not, so can provide real criticism only sporadically, relegating my remaining comments to expressions of admiration or boredom.

Robert E. Ricklefs opens the volume with a masterful review of growth entitled "Avian Postnatal Development." He takes Margaret Nice's linear spectrum from precocial to altricial birds as his rallying point, apparently missing or ignoring my criticisms of it (in Farner, 1973, Breeding Biology of Birds, pp. 22–27), or else choosing to ignore it. Ricklefs sees the young's type of food as "the overriding factor in establishing the precocial-altricial spectrum" (p. 10), but it is not clear how he decided chicken from egg in this correlation. He does, however, make a good case for asserting that the advantage of the altricial condition is rapid growth. I found an interesting part of this chapter to be that on equations for growth (pp. 30–43), the section constituting an exemplary general case for anyone interested in mathematical descriptions of biological processes. In his genetical section Ricklefs is suspicious of high heritability values reported for various characters of several wild species, a point on which I heartily concur. In the end, he concludes that interspecific variation in growth rate is related to precocity and final body proportions rather than direct environmental effects on individual characteristics, and hence reinforces my favorite biological dictum that "everything is connected to everything."

Susan M. Smith contributes a competent overview of avian behavioral ontogeny, using a hazy continuum between "innate" and "learned" as endpoints (p. 88). I would have hoped for more trenchant criticism of Robert Hinde's views, such as his objection that "innate" is defined by exclusion as "unlearned." If one must think superficially in dichotomous terms, surely the proper ploy from logic is to divide into "X" and "not-X," so Hinde must have had a deeper objection in mind. Nowhere in this chapter is there discussion of experience at one activity that potentiates the development of another, as in practice standing in gull chicks that facilitates pecking accuracy. Still, the romp through behavior of embryos, hatching behavior, imprinting, song development, feeding, orientation, and play makes this a most useful review. I noted that the reference to "Harth (1971)" on p. 93 is to be found in neither the bibliography nor the author index, and the chapter has a sprinkling of typos that might have been caught (e.g., "experince" on p. 99 and "uestion" on p. 109). Smith is a good critic in restricted areas where she has experience, such as of the "critical period" non-issue (p. 104), interpretation of stimulus-complexity (p. 106), sexual vs social issues (pp. 110–111), and so on. However, much is missed, such as Schutz's (1965) claim for sex differences in imprintability (p. 111) being confounded by his having imprinted male and female ducklings at different ages, Bateson's (1978) theory being not so much the prevention of inbreeding depression (p. 112) as the selection of mates for optimum genetic similarity, and my experiments showing not that clasping (p. 126) but rather head-rotation is the learned

motor component in gull chick pecking. In sum, the strength of this chapter is its breadth rather than depth, and it should prove an invaluable roadmap for anyone studying comparative aspects of ontogeny.

Glenn E. Walsberg presents a surprisingly data-packed review of the relatively new science of ecological energetics, although it may be true that more interesting questions are raised than answered. Allocation of daily total energy includes about 10% to territorial defense, negligible amounts to testicular growth (and likely sperm production) of the male during the nesting season, and minor amounts for ovarian and oviducal growth in the female. Egg-synthesis, as one would expect, is costly but variable from perhaps 50% of the basal metabolic rate in small passerines to twice the BMR in larger birds such as ducks. The energetic costs of incubation are clearly controversial and Walsberg finds evidence for an actual "decrease in resting metabolism in an incubating bird compared to that of a bird outside of the nest in its normal microclimate" (p. 183). Molt requires a substantial energy expenditure and in general sheer maintenance of the body may require as much metabolic power as all other activities combined. I lament the exclusion from this chapter of thermal energy exchanges with the environment, the review included in Calder and King's chapter of an earlier volume now being woefully out of date a decade later. And I wish the chapter had dealt with issues such as claims that metabolic chambers give spurious results due to the fact that radiation from the bird and back to it from the chamber have not been accounted for. Such issues affect baseline values used for comparisons in ecological energetics. But it is never wholly fair to complain about what is absent, and in this case what is there is a superb attempt to wrest the best interpretation from available data.

Jacques Balthazart provides an immense tome (144 pages) on "hormonal correlates of behavior," which is to say principally reproductive behavior. Removal of endocrine sources such as the testes and replacement therapy such as testosterone injection classically secured the androgenic basis of male sexual behavior and the estrogenic basis of female sexual behavior. Nest-building, incubation, and brooding and feeding the young have more complexly determined bases, however, and a number of questions remain unresolved. Balthazart carefully reviews methodological problems in determining hormonal action, and goes on to identify the revolutionary effects on measuring hormone titers brought on by the advent of radioimmunoassay. There is an extensive consideration of brain mechanisms of endrocrine function. I am no expert in this field, but if Balthazart's chapter is not a classic review, I'll eat the bibliography (which is no small task, as it runs 30 pages of small print).

Robert L. Rausch has competently provided more than most ornithologists will ever want to know about helminth parasites of birds. The most important avian parasites are protozoans, arthropods (such as mites, ticks, and various insects), and helminths, which is to say "worms." These last fall into three phyla: Platyhelminthes (trematodes and cestodes), Aschelminthes (nematodes), and Acanthocephala. Rausch remarks that, "The literature concerning helminths in wild birds is so extensive that it obscures the limitations that exist in our knowledge of this group of organisms" (pp. 367–368). The best surveys, it seems, come from the Soviet Union. The chapter reviews the helminths, compares Rausch's own North American surveys (made in the 1940's) with those summarized from the literature, reviews infections by orders and families of birds, discusses the problem of host-specificity, recounts how birds become infected (mainly through eating infected organisms), and mentions where helminths are found inside the birds. In the jargon of the practical man, the "bottom line" is provided by Rausch's very last sentence (p. 432): "On the basis of present knowledge, most helminths must be regarded as symbiotes that have no discernible adverse effect on their avian hosts."

Bruce Glick recounts what must be nearly every known fact about the bursa of Fabricius

in a jargon-filled chapter that explains its subject in the first sentence as ". . . a dorsal diverticulum of the proctodeal region of the cloaca." The bursa grows and then regresses in the domestic chick. In 1954 then graduate-student Glick removed bursas during the growth phase but saw no obvious adverse consequences on development. Fellow student T. S. Chang used the birds for a class demonstration of antibody production to *Salmonella* antigen, which demonstration failed and hence led to the discovery of the bursa (first described in 1621 in a posthumous publication of Fabricius) as having a central role in immune responses.

Only an ornithologist with more catholic interests than mine could possibly want to own this volume of potpourri—except to complete his or her set of "Avian Biology," an exception presumably restricted to the rich. However, the authoritativeness of its content makes volume VII a mandatory addition to every university library.—Jack P. Hailman.

Weather and Bird Behaviour. By Norman Elkins. T. and A. D. Poyser, Calton, England, 1983 (distributed in North America by Buteo Books, Vermillion, South Dakota): 239 pp., 16 black and white plates, 50 numbered text figs., 5 tables. $32.50.—More than any other animals, birds have become the relative masters of the air. Spending so much time in the atmosphere, it is not surprising that their lives are heavily influenced by its short-term dynamics, weather. Norman Elkins is a meteorologist by training, an ornithologist in his spare time. Here he has provided a relatively non-technical introduction to weather, its causes and dynamics (as opposed to climate), and a compendium of all of the ways in which weather and birds interact. Following a 16-page crash course in meteorology, there are 11 chapters detailing flight, feeding, aerial feeding, breeding, comfort, migration, vagrancy, soaring birds, effects of extreme weather, and seabird biology.

I found the book clear, and in most parts, interesting to read. It contains literally hundreds of examples as documentation of its general points and they are both boon and bane. Such detail makes for dry reading and in spots there are too many examples and not enough synthesis to tie them together. Nearly all of the examples are drawn from Europe, especially Great Britian. North American readers may be confronted with many unfamiliar place names and perhaps unfamiliar bird species. On the other hand, there is a nice summary of the weather conditions associated with the arrival of North American vagrants in Britain, based mostly on Elkins' own research into the matter.

The book was obviously not intended to be a technical treatise and so one should not expect extensive documentation of statements. Nonetheless, I found the handling of the literature frustrating. The bibliography contains 195 references, cited by superscripted numerals in the text, but citation is very uneven and there were many intriguing statements for which I would like to have known the source. Some unwarranted generalizations are inevitable in a book of this type, but I noted few and the occasional unfounded statement (e.g., that flocks show better navigational ability than single birds, p. 113) does not detract seriously from the thrust of the text.

The volume is nicely produced, the text enhanced by numerous attractive pen and ink drawings by Crispin Fisher. Both Elkins and the publisher can be pleased with the product.—Kenneth P. Able.

Pigeons and Doves of the World. Third edition. By Derek Goodwin, illus. by Robert Gillmor. British Museum (Natural History) and Cornell University Press, Ithaca, New York, 1983:363 pp., 6 color plates, many line drawings and maps. $48.50.—Neither the first (1967) nor the second (1970) edition of this book was reviewed in The Wilson Bulletin. I will therefore write a somewhat longer review than would be usual for a third edition. A rather

short, mostly descriptive review of the first edition was published by N. Collias (Auk 86: 151–152, 1969).

To review briefly the history of this book, the first edition was issued in 1967 as Publication no. 663 of the British Museum (Natural History), hereafter BM(NH). The second edition (1970) is identical in format to the first, and has no separate introduction or foreword to explain what changes, if any, had been made in this edition. In 1977 the BM(NH) published a 33-page addendum to the second edition, based on recent literature, information sent to the author, and his own field and aviary observations.

The edition under review, the third, is genuinely new, and, of course, incorporates all of the information in the 1977 supplement. Although the BM(NH) still holds the copyright, the publisher of record is "Comstock Publishing Associates, a division of Cornell University Press." The text has been completely reset in double column format, in a slightly smaller but perfectly legible typeface. The amazingly productive Bob Gillmor has supplied three additional color plates: Snow Pigeon (*Columba leuconota*) and various rock pigeons (*C. rupestris* and *C. livia* subsp.); fruit doves (*Ptilinopus* sp.) of New Guinea; and seven "actually or potentially endangered island species." The color reproduction of the three original plates is somewhat crisper (so that, for example, tarsal scutellation is easier to see), but the colors themselves have changed. The male Maroon-chested Ground-Dove (*Claravis mondetoura*) of plate 2, for example, has lost what was an unwarranted pinkish tinge, but is now far too pale. The plates are scattered through the first 50 pages of the book; unlike earlier editions, the table of contents lacks a list of plates.

At the end of each genus and species account is a list of pertinent references; these are easier to read than in earlier editions, as the authors' names have been set in boldface. However, the change is purely cosmetic; an obvious error in pagination in the first reference under the Dusky Turtle-Dove (*Streptopelia lugens*) ("297–239," should be –329) has been carried in all three editions. Some references omit the paper title or even the year of publication; some of these omissions are carried over from the previous editions, while others occurred during the resetting of type.

The most serious criticism that can be made of this edition is in its perfunctory coverage of literature. In his review of the first edition, Collias (1969) called attention to "a few surprising omissions" in the author's use of the literature. No closing date for the 1983 edition is given. However, in going through the entire book, I found only 7 references dating from 1979, one from 1980, and two from 1981. A paper by W. N. Beckon is cited on p. 305 as "in press," but on p. 306 as "1979, in press." The Zoological Record volumes for 1979 and 1980 list 11 and 4 papers, respectively, on non-European species of Columbidae that might well have merited citation by Goodwin. The Zoological Record volumes for 1981 and 1982 are not yet available, but will probably contain comparable numbers of papers on Columbidae not cited by Goodwin. That he did look at literature as recent as 1982 is indicated by his citation on pp. 56 and 63 of a 1982 paper in a German journal.

Some of the text changes have had awkward consequences. In earlier editions Goodwin included the endangered Pink Pigeon of Mauritius in the genus *Columba*. Based on recent behavioral studies, he now feels that "its closest relatives seem likely to be in *Streptopelia* and it seems best to recognise, provisionally, the monotypic genus *Nesoenas*." Although the caption of the adjacent dendrogram has been altered to read "Presumed relationships within the genera *Columba* and *Nesoenas*," there is no indication on the dendrogram itself, reprinted intact from earlier editions, as to which former species of *Columba* has been transferred to *Nesoenas*. The adjacent text does not help, as Goodwin does not mention the specific name of the Pink Pigeon. One must find the species account, 55 pages later, to learn that the transferred species is *mayeri*.

It is, of course, impossible to monitor all of the factual material in a compendium of this

sort. By pure chance, when checking on the erroneous page number under *Streptopelia lugens* mentioned above, I found that the paper cited (Cheesman and Sclater, Ibis 1935: 308) mentions eggs of *S. lugens* found on 13 September. Goodwin cites this paper under "Display," but overlooked its egg data in an adjacent paragraph, as he gives the breeding season as "most months between December and June inclusive (Mackworth-Praed and Grant, 1957)." I admit that this is just one small slipup, but in such cases one always finds oneself wondering how carefully the literature was used elsewhere in the book.

There is no question at all about the authoritativeness of Goodwin's own observations in the field and in the aviary. He has long been a serious student of the comparative behavior of the Columbidae, and his first-hand accounts of voice and displays are among the most valuable aspects of the text. Collias (1969) called attention to the lack of spectrograms of pigeon vocalizations in the first edition. There are none in the present edition either, as Goodwin believes (p. 29) that transcriptions of bird calls by means of letter combinations, although they have shortcomings, are more useful to most readers than are sound spectrograms (sonagrams).

Goodwin's book continues to be the most convenient single source of information on the Columbidae in spite of its minor shortcomings, and readers wishing further details or verification of data assembled by Goodwin will in any case wish to consult the primary literature. Libraries lacking a copy of either of the previous editions should without question buy this one; whether one should spend $48.50 to add the moderate amount of new information in the third edition to a library that already has an earlier edition is doubtful.—KENNETH C. PARKES.

WEST VIRGINIA BIRDS. By George A. Hall. Carnegie Museum of Natural History Special Publication No. 7, Pittsburgh, Pennsylvania, 1983:180 pp., 1 color plate, 21 black-and-white plates, 10 range maps and 2 state outline maps, and 16 unnumbered black-and-white drawings. $20.00.—In the foreword to this book, George Hall expresses the hope that this work will serve as a benchmark for future generations. In my view he has done this and more: authors of new state or regional books may look to this one as the standard, for it is much more than a list of where birds occur. Hall begins with a careful account of the geology and geography of West Virginia. This is followed by a history of ornithology in the state. It is a fascinating account of the contributions of many people (including those with names like Brewster, Brooks, Sutton, Wetmore, and Wilson), and the Brooks Bird Club. The third section is a faunistic analysis of the physiographic and ecological factors in bird distribution, as well as of trends in habitat change and species distribution and abundance through time. Among other things, one learns which species fit into "neat patterns" of distribution and which (e.g., Black-throated Green [*Dendroica virens*] and Golden-winged [*Vermivora chrysoptera*] warblers) do not. Hall urges caution in inferring past from current distributions, in light of the massive impacts of early clearing, recent reforestation and strip mining. His discussion of West Virginia's location at the northern limit for certain species, and the southern limit for others is enlightening. Indeed, all three sections merit careful reading, because they form a basis for understanding species distributions in this complex region, and for appreciating the contributions of many past and present ornithologists (quiz: how many in or outside the state know for which Brooks the Club is named?).

The fourth section consists of the species accounts, and these are painstakingly thorough. The accounts contain notes on the general status, seasonal occurrence, breeding records, bracket migration dates, and location of known specimens. The new A.O.U. Check-list names and sequence, metric measures, and Celsius temperatures are used throughout. Some readers

may object to the latter aspects (as well as to the former), but these must be the standard usages in ornithology from now forward.

There are insightful discussions of difficult taxonomic matters: for example, Hall's treatments of the Traill's flycatcher (*Empidonax traillii, E. alnorum*) complex, Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers, and the Red Crossbill (*Loxia curvirostra*) are impressive. However, referring to hybrid warblers by their old binomials seems unnecessary, and calling the Lawrence's form a "pure recessive" (p. 118) may only serve to perpetuate old myths about birds for which no proper genetic analysis has been done. He correctly draws attention to the great variation among the putative hybrids, but the only trait that looks like a simple Mendelian effect is the presence or absence of throat markings. I also found the designation of populations and individual specimens by subspecies of doubtful use in some cases, as some "races" represent extreme ends of clinally variable forms (e.g., Pine Grosbeak [*Pinicola enucleator*]), or are invalid for other reasons.

Hall writes with authority, drawing from a huge data base and long experience. He examined most of the specimens known from the state, including those in 15 public and 3 private collections, has some 34 years of field experience in most of the counties, and has been a regional editor for American Birds for many years. The difficult matter of describing relative abundance of species is handled well: the categories are based on how many individuals of a species one may expect to see in a day's field work. Thus one may see between 51 and 100 of a very common species, or only 1–6 of an uncommon species, etc. These categories are supported by abundance data from Breeding Bird Surveys, Singing Male Censuses, banding, and Christmas Counts.

This book is, thus, a logical outcome of decades of painstaking research and documentation by the author and many others. It is printed on high quality paper and is well bound. There are virtually no typesetting or other errors. The drawings of some of the species by the late George M. Sutton add much to this very scholarly work, and the frontispiece, a reproduction of Sutton's watercolor of Sutton's Warbler (*Dendroica "potomac"*), is superb. Its large size makes it an unlikely field companion. Rather, it is an essential library reference work for field and museum workers alike. Publication was partly supported by the Nongame Wildlife Program of the West Virginia Department of Natural Resources, which no doubt contributes to the book's affordability.

West Virginians will certainly profit from this foundation as they embark on their Breeding Bird Atlas project. Ornithologists elsewhere, and especially in the Appalachian Mountains, will benefit nearly as much, because it points the way to a faunistic approach which can be emulated by others. For instance, it is a far greater contribution for forays or sorties to explore truly unknown, if less exciting, areas than the known but reliably exciting birding areas. There are many places in the mountains which are as "wild and wonderful" as is West Virginia, and less well known ornithologically. West Virginia Birds is thus not only a benchmark for the state, but potentially the keystone in a larger set of knowledge of the birds of the Appalachian Mountains.—Curtis S. Adkisson.

Birding in Ohio. By Tom Thomson. Indiana University Press, Bloomington. 1983:256 pp., numerous unnumbered maps throughout. $15.00.—As the title suggests, the first two thirds of this volume is devoted to a birding site guide. Over 200 locations are described in brief and directions are provided for finding each site. The species likely to be encountered at each are also noted. There are key maps at the beginning of each of three sections and scattered throughout the text are numerous other maps. These maps are a most useful addition to the book yet are perhaps the area of greatest concern. Most are clear and legible

although a few appear somewhat small and cluttered (p. 18) or suffer from poor printing (p. 19). And I think the usefulness of the maps could have been enhanced by more thorough cross-referencing. For example, to find Metzger Marsh (listed on p. 38) one is directed to map A-53. However, no page number is given for this map (it is on page 4—a page with no page number), but the location of this marsh is also set out even more clearly on the map on p. 10, to which no reference is made at all. This section does, however, provide a comprehensive listing of birding sites that will be useful to anyone birding in the state.

What is not evident from the title is that about one third of the book is devoted to an up-to-date annotated checklist of the birds of Ohio. This section lists information on the occurrence and abundance at various times of the year and an indication of breeding for all species recorded in the state. Care has been taken to define terms used in the text. Historical information and some details of unique sightings are also included. This section appears to be comprehensive, accurate, and a very useful summary of Ohio's bird life. Such a compilation has not been available for many years and it is unfortunate that this section was not noted in the title.

I would recommend the book to anyone with an interest in birds or birding in Ohio. The price seems modest for this hard covered book.—Ross D. James.

Where to Find Birds in British Columia, 2nd Edition. By David M. Mark, illustrations by Linda Miller Feltner. Kestrel Press, New Westminster, British Columbia, 1984:122 pp., 15 black-and-white illustrations, 16 maps. Paper cover. $6.95 Cdn.—This is the second edition of a standard reference for birders visiting or resident in British Columbia. Following a concise introduction to the variety of biotic zones and the birds typical of each, the text provides information on birdwatching at 81 selected sites throughout the province. The sites are organized into eight regions which roughly correspond to the distinct biotic areas. In a clear and readable style the author and contributors describe how to locate and observe birds at each site. Emphasis is given to finding the more sought after species of each area. Most sections appear to be entirely re-written and updated versions of those of the first edition, with 32 new sites in this edition. Elegant maps of each region and several sites are provided. Site descriptions appear to be generally accurate, although an enthusiastic discussion of the birding possibilities of a ferry between Prince Rupert and the Queen Charlotte Islands fails to mention that the crossing takes place only at night! Horned Puffins (*Fratercula corniculata*) are mentioned as being breeders in the Queen Charlotte Islands; however, there is in fact no confirmed evidence of breeding of this species in Canada. The 15 excellent line drawings compliment the text and add greatly to the attractiveness of this book. Bird listers will appreciate the annotated checklist and "sought-after species guide." In this section each species is indexed to areas mentioned in the text and notes on finding the more rare and local of British Columbia's birds are provided. A short bibliography lists titles concerning birdwatching and bird distribution in the province. This well produced book is a must for anyone planning to watch birds in British Columbia. Copies may be obtained from: Kestrel Press, P.O. Box 2054, New Westminister, British Columbia, Canada V3L 5A3.—Ian L. Jones.

Birds New to Britain and Ireland. Edited by J. T. R. Sharrock, commentary by J. T. R. Sharrock and P. J. Grant, illustrations by 18 artists. T. & A. D. Poyser Ltd., Calton, England, 1982:263 pp., 81 black-and-white photographs, 94 line drawings, 83 range maps, 22 figures, 3 tables. $25.00.—This book, like its predecessor "Frontiers of Bird Identification" (edited by J. T. R. Sharrock, MacMillan London Ltd., 1980) is essentially a repackaging

of material that has already appeared in British Birds. Presented here are the original accounts of the 83 species added to the British and Irish list from 1946–1980. The original versions have been left intact except for a few minor nomenclatural changes, but three things have been added: (1) the current status of the species (number and distribution of additional occurrences); (2) a simplified world range map to show how far the bird must have travelled; and (3) a summary by ace field man Peter Grant of identification points not covered in the text.

One might wonder why this material, already possessed by subscribers to British Birds and available in most ornithological libraries, is reproduced here. A primary purpose, in the words of the editor, a self-confessed rarity-chaser, is "to collect together in one place all of the most memorable, sensational and exciting moments in the past 35 years of rarity hunting." It is refreshing to see a professional ornithologist like Dr. Sharrock freely admit to his predilection, unlike the closet listers in North America afraid for their professional reputations. Running after rare birds is a popular sport in North America; witness the stampede to see the Ross's Gull (*Rhodostethia rosea*) at Newburyport, Massachusetts, in 1975. But through an accident of geography vagrants occur much more often in Britain and form a much higher percentage of the avifaunal list, and birds new for the country are added more frequently. Most are readily accessible, except on a few of the outer islands. In North America few have time or funds to fly off to see a La Sagra's Flycatcher (*Myianchus sagrae*) in Florida or an Aztec Thrush (*Ridgwayia pinicola*) in Arizona. In Britain it is no trick to see every breeding species and regular migrant in a single year (except for a few extreme rarities whose whereabouts is kept secret as a precaution against egg-collectors); so for keen birders, combing the country for vagrants soon becomes the only game in town. In North America many go through a lifetime without even seeing all our breeding species (who has seen Wood Sandpiper [*Tringa glareola*]? Siberian Tit = Gray-headed Chickadee [*Parus cinctus*] Bluethroat [*Luscinia svecica*]?).

A second objective is the publication of extensive reference material on each species. Any bird suspected of being new to Britain and Ireland is subjected to the most intense scrutiny. Extremely detailed accounts are required, and these are examined first by the county records committee, then by the national British Birds Rarities Committee, and lastly by the B.O.U. Records Committee. As a result, far more detail is published than is available in most bird books, much of it new, and in some cases these remain the basic references for the species for many years. Definitive characterizations from the present work include Moustached/Sedge warblers (*Acrocephalus melanopogon/schoenobaenus*), female Baikal Teal (*Anas formosa*), Thick-billed Warbler (*Acrocephalus aedon*), Cretzschmar's/Ortolan buntings (*Emberiza caesia/hortulana*), Pallas'/Common reed buntings (*Emberiza pallasii/schoeniclus*), Pallid/Common swift (*Apus pallidus/apus*), and Ringed/Semipalmated plovers (*Charadrius hiaticula/semipalmatus*).

Perhaps the chief interest of this book for North American readers will be the New World species; 47 of the 83 new species come from this side of the Atlantic. More significant is the number of subsequent occurrences. The following occurred 10 or more times between 1946 and 1980:

Wilson's Phalarope (*Phalaropus tricolor*)	129	Blackpoll Warbler (*Dendroica striata*)	15
Ring-necked Duck (*Aythya collaris*)	120	Stilt Sandpiper (*Calidris himantopus*)	12
Ring-billed Gull (*Larus delawarensis*)	37	Grey-cheeked Thrush (*Catharus minimus*)	12
Semipalmated Sandpiper (*Calidris pusilla*)	26	Northern Oriole (*Icterus galbula*)	12
Laughing Gull (*L. atricilla*)	26	Black Duck (*Anas rubribes*)	11
American Robin (*Turdus migratorius*)	23	Red-eyed Vireo (*Vireo olivaceus*)	10

These statistics cover only the new birds on the British/Irish list; there has been a tremendous increase in sightings of all North American birds, many already being on the list by 1945. This does not represent an invasion of western Europe by North American birds but reflects the increase in banding stations and bird observatories, and in numbers of birders and thus greater coverage. One is reminded of the apparent "invasion" of California in the last decade by "eastern" birds, uncovered by an army of eager birders.

This book undoubtedly has greater appeal for British than American audiences; nevertheless students of trans-Atlantic vagrancy or of fine points of bird identification will find much to interest them.—STUART KEITH.

A NATURAL HISTORY OF BRITISH BIRDS. By Eric Simms, illustrated by Robert Gillmor. J. M. Dent and Sons, 1983:xiv + 367 pp., 16 colored plates, 137 black-and-white figures. $24.95.—In this well written and enjoyable book Eric Simms covers a large variety of topics, including many that would not commonly be considered natural history. Besides chapters on feeding, vocalizations, behavior, breeding, nesting, and migration, there are ones on fossils, anatomy, birds in art and literature, and more. There are also various practical ones on where to find birds, how to watch them, and the environments in which to find different ones. Naturally, with such a range of topics, most are treated but briefly and sometimes quite superficially. However, I noted very few things that I would quibble with; the brevity results in the omission of points I would like to see made, but not in the oversimplification of those made. Another consequence of trying to cover so much is that lists are often resorted to. That of the birds of Great Britain and Ireland is useful and basically an appendix, but the extensive one of classic localities for various habitats would be more frustrating than enlightening for somebody without further information on where these localities are and how to reach them (e.g., coastal lagoons are listed as "Chesil Fleet, Slapton Ley, Havergate [RSBP], Loch of Strathbeg [RSBP], and in Ireland at Malahide, North Bull, Kilcoole and the Murrough").

The illustrations by Robert Gillmor definitely enhance the value of this book; indeed the author notes that the justification for this book may lie "firstly, in the brilliantly informative and evocative illustrations." That may be an overstatement, but it is not an outrageous one. The black-and-white figures are not numbered or commonly referred to in the text, but they are usually in the appropriate place and definitely serve to supplement and explain the writing; they are excellent. The colored plates are, in my opinion, slightly less successful, and they are certainly less useful with regard to the text. They are, with one exception, never referred to, are not near the appropriate parts of the book, and are difficult to interpret. For this the publisher's editorial staff must take most of the blame. If, for example, I look at Plate 1, I see a variety of birds identified at the bottom of the page. However, I can discover that this is intended to show "Birds of the summer oakwoods" only by finding a list of plates between the contents and the dedication; there is no general caption under the plate and it is never referred to in the various discussions of the birds found in such forests. Gillmor's work deserves better treatment.

For somebody in the British Isles wanting one book on most aspects of birds and bird-watching not covered in a standard field guide, this would be an excellent choice. However, for others it is far less appealing. Virtually all examples are of British birds, the only environments considered are those in Britain, the addresses of clubs are only of British ones, and the localities mentioned are all British. Even the artists and writers noted are almost all British. After Audubon's "Birds of America" (1827–38), some 29 painters of birds are mentioned; virtually all are British and only one is American—Roger Tory Peterson, presumably because of his "Field Guide to the Birds of Britain and Europe." The musicians

who imitated birds are from all over Europe, but even here only those using calls of birds found in Britain are noted. Even the bibliography stresses British work and omits many, though not all, useful American references. Such insularity is not, of course, necessarily a weakness of the book and it is implied in the title; however, it certainly does lessen its appeal and value for North American and other non-British readers.—Thomas S. Parsons.

Birds of Prey of Britain and Europe. By Ian Wallace, illustrated by Ian Willis. Oxford University Press, Oxford and New York, 1983:viii + 88 pp., 43 colored plates (on 33 pp.). $15.95.—This book consists of the colored plates of raptors from Vol. 2 of Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic (1980), already reviewed in this journal (S. Keith, 1981, Wilson Bull. 93:430–432), plus a rather general text of 19 pages and comments on field identification facing each plate. The plates are excellent and the text good, but I really fail to see much use for this book for any serious student of raptors or other birds. It would serve as a useful set of color plates to accompany the excellent book by Porter et al. (Flight Identification of European Raptors, 3rd ed., 1981), but any reader interested in aspects other than field identification will wish to own the full Handbook. Granted this new book costs considerably less ($15.95 instead of $85.00), but you get considerably less: 52 pages of text (not counting introduction, indices, and the like) versus 683, 33 pages of colored plates versus 69, and no maps, sonograms, or black-and-white drawings illustrating behavior versus hundreds of them. This is not to say that Birds of Prey of Britain and Europe is a poor book; it is a very good one. However dollar for dollar Vol. 2 of the Handbook is, I think, a better buy.—Thomas S. Parsons.

The New Guide to the Birds of New Zealand. By R. A. Falla, R. B. Sibson, and E. G. Turbott, illustrated by Elaine Power. New Zealand Ornithological Society, 1978 (reprinted with Addenda 1981, 1982):247 pp., 48 color plates, 2 monochrome plates, 9 line drawings, 3 maps. $17.95.—Every ornithologist contemplating a visit to New Zealand or with an interest in birds "down under" will want to purchase a copy of this revised and enlarged version of the original field guide published in 1966. In responding to criticisms from novices about the need for more assistance in the identification of species, for the new edition the authors and publisher commissioned local bird artist Elaine Power to paint 48 new full-color plates to replace the old ones by Chloe Talbot Kelly. Some monochrome plates and line drawings have been retained, and thus virtually all 300 species of the New Zealand region from the Kermadecs in the north to Macquarie Island in the south are illustrated.

The color plates alone are worth the price of the book, and greatly facilitate species identification. For example, anyone who has seen groups of mollymawks wheeling over stormy seas and has tried to identify Black-browed (*Diamedea melanophris*), Yellow-nosed (*D. chlororhynchus*), Buller's (*D. bulleri*), and Grey-headed (*D. chrysostoma*) species which are not only similar in appearance as adults but also have confusing immature plumages, will greatly appreciate the lovely new color plate 6 which clearly distinguishes age classes and species.

The text is much more attractive in the new guide because it has been completely reset in larger format and is also extended to include additional extralimital species. Each species is described in standard format with information on its size, plumages, general appearance, voice, habitat, range, and breeding habitats. I heartily recommend this attractive new guide to professional ornithologists, birders, and lay public—there is something in it for everyone.—Allan J. Baker.

BIRDS AT A GLANCE. By Lou Blachly and Randolph Jenks, illus. by Sheridan Oman. Van Nostrand Reinhold, New York, New York, 1984:xv + 327 pp., many black-and-white drawings. $13.50 (paperback).—This is an apparently unrevised paperback edition of a book originally published in 1963 under the title, "Naming Birds at a Glance." The method of identification consists of a series of keys based on color characters and combinations for which the observer may have only fleeting glances. The method does work for those species included. However, only "common" landbirds in the area from South Carolina to the Rockies and north to the Arctic are included. The scope is further limited in that all female and autumn plumages, where these differ from spring males, are omitted. As Robert Arbib remarked in his review (Wilson Bull., 76:302–303, 1964), "Thus the system rules out about 75 percent of the individuals the bird watcher will see throughout the year!" This review supplies a more detailed critique of the book. It is difficult to see any reason for the reissue of this book at this time, but perhaps some beginners might find it useful.—GEORGE A. HALL.

WINGTIPS (New periodical). Helen S. Lapham, Publisher and Editor, Box 226, Lansing, New York 14882, 1984. $10 per year.—The stated goal of this new quarterly is to serve as an "information source for what is happening in ornithology today." "Wing Tips will communicate with amateurs (and professionals), involving anybody who wishes to enrich their ornithological background." The first number has 65 pages, mostly devoted to a discussion of the sixth edition of the A.O.U. Check-list, but also including some book reviews and a handy list of meeting dates. If further numbers maintain the present standard most Wilson Society members will find this a useful and informative publication.—G.A.H.

DICTIONARY OF THE ENVIRONMENT, 2nd edition. By Michael Allaby, New York University Press (Distributor: Columbia University Press, New York, N.Y.), New York, 1983:529 pp. $50.00 (hard cover).—A dictionary is useful only if it is readable, current and easily accessible. The new edition of this book is every bit as readable as the first. The definitions are concise and clearly stated. In fact, most of the original entries remain unchanged. The author has concentrated instead on bringing his dictionary up to date. He states in the preface that the main changes reflect both the attitudes and concerns of environmentalists and the developments in the life and earth sciences. Since 1977, many new environmental issues have emerged and subsequently, new terminology. Other terms that were once in prominence and now rarely or never used have been removed.

Deciding which terms to include or remove is a difficult and somewhat arbitrary task. The removal of seemingly archaic terms from a dictionary poses a problem. A person reading an early paper on a topic may encounter the very archaic term omitted from the latest edition. Hence the old rather than the new edition is more useful for that reader. Removing such terms defeats the purpose of a dictionary.

To be fair, more has been added than removed, with the new edition having five additional pages. The author has responded to increasing interest in nuclear power issues and recent advances in earth sciences resulting from ocean floor core samples by updating and adding the appropriate entries. The new terms include nuclear fuel cycle, Three Mile Island, euhaline, zoogeographic regions, and ZPG. Some items were tidied up in the new edition. For instance, generic names are now italicized. Some long explanations have been revised and de-emphasized. The full page diagram accompanying the Citrc Acid Cycle, for example, has been removed. More biological taxonomic groups have been added although the inclusion of bird families appears to be half-hearted. Many non-passerine families are defined, yet not even

the "Fringillidae" among the passerines warrants an entry. One term in both editions that is either an inside joke or has escaped proofreading is the definition: "Environment, Department of" as "Department of the Envoirnment (sic)."

Many hormones listed in the first edition have been retained, but ACTH, ADH, noradrenaline and the adrenal gland have been removed. If hormones are included because of their effects on an organism's internal environment, it is puzzling why the effects of adrenaline or the role of the adrenal gland are considered superfluous.

In spite of the above criticisms, this book is a useful reference. It is readable and relatively up to date. That leaves the question of accessibility. Conservationists, scientists, and students of any discipline associated with the environment will benefit by having this new edition if they are willing to pay $50.00 for it. It is certainly not that much of an improvement to warrant owners of the first edition purchasing it. Students, the people least likely to be familiar with the terminology and hence the prime potential users, are unfortunately the very ones who can least afford to pay the price. Their only hope is to find it in their local library.—Allan Werden.

Microbiology: Fundamentals and Applications. By Ronald M. Atlas. Macmillan Publishing Company, New York, 1983: xxi + 988 pp., 12 colour plates, numerous figs., tables, black-and-white photographs and illustrations. $34.95.—At a time of growing interest in genetics, topics such as regulation of gene expression, genome structure, genetic exchange and recombination, genetic mapping and genetic engineering are adequately covered in this text for the undergraduate. Emphasis is on the prokaryotic microorganism; however, comparisons are found between them and eukaryotic organisms. The book also includes diverse topics such as medical, food, industrial, and environmental microbiology.

Although this book was written for introductory microbiology and bacteriology courses, I highly recommend it to anyone interested in microbiology and its applications. This book is clearly written and the illustrations are, on the whole, interesting and contribute greatly to the overall impression of the work.—Carol M. Edwards.

McGraw-Hill Concise Encyclopedia of Science and Technology. Sybil P. Parker (Ed. in Chief). McGraw-Hill Book Co., New York, New York, 1984:lxxiv + 2064 pp., many photos and line drawings. $89.50.—This is an impressive and invaluable reference work. All entries are written by authorities and are at quite a high level. While there are numerous entries on biology, ornithology and birds are scarcely mentioned. However, it is highly recommended for libraries (both high school and university).—G.A.H.

PROCEEDINGS OF THE SIXTY-FIFTH ANNUAL MEETING

CURTIS S. ADKISSON, SECRETARY

The Sixty-fifth Annual Meeting of The Wilson Ornithological Society was held Thursday, 31 May to Sunday, 3 June 1984 at the University of North Carolina–Wilmington, in Wilmington, North Carolina. The meeting was held jointly with the annual meeting of the Carolina Bird Club, and was hosted by the University and by the Lower Cape Fear Bird Club. Dr. James Parnell chaired the Local Committee on Arrangements, which consisted of: Bill Adams, Walter Biggs, Robin Bjork, Jane Bracket, Dick Dillaman, Dargan Frierson, Mark Galizio, Courtney Hackney, Julie Hovis, Kitty Kosh, Jan Sumerel, Greg Massey, Frances Needham, Mark Shields, David Webster, Bill Woodhouse, and Sally Zimmerman.

The meeting began with a wine and cheese reception for participants at the University Union on Thursday evening. Friday there were early morning field trips, after which the First Business Meeting was held. The Society was welcomed by Dr. Daniel Plyler, Dean of Arts and Sciences. President Jerome A. Jackson responded for the Society. After the first business meeting, the paper sessions began.

There were several memorable events, in addition to the scientific paper sessions, during the meeting: a wine and cheese reception was held in the courtyard of the University Union Thursday evening; on Friday evening a Shrimp-a-roo, a local specialty featuring dining on boiled shrimp at the beach, was held at the Ft. Fisher Marine Resources Center; there were films, and also a display of wildlife art by Carolina artists; the spouses' program included tours of Poplar Grove Plantation, the Wilmington waterfront area, the battleship U.S.S. North Carolina, and historic homes of Wilmington. Workshops on several ornithological topics were a special attraction of this meeting. These workshops and their leaders were: bird photography, by Ken Taylor; raptor rehabilitation, by Richard Brown; seabird identification, by David Lee and Gilbert Grant; and techniques of wood carving, by Neal Conoley.

Field trips to local birding areas were organized every morning of the meeting. On Sunday, there were trips to the Green Swamp, to the Lower Cape Fear River, and to Holly Shelter, as well as a day-long pelagic cruise.

The annual banquet was held on Saturday night in the University Union. After the banquet John Henry Dick presented a program on wildlife of India.

At the banquet, President Jackson announced these awards:

EDWARDS PRIZES (for best papers appearing in *The Wilson Bulletin* in 1983)

Two equal awards were given to:

Peter M. Fetterolf, "Effects of investigator activity on Ring-billed Gull behavior and reproductive performance," Wilson Bull. 95:23–41.

John L. Zimmerman, "Cowbird parasitism of Dickcissels in different habitats and at different nest densities," Wilson Bull. 95:7–22.

MARGARET MORSE NICE AWARD

Sharon L. Milder, "The natural history of *Acrocephalus aequinoctialis*."

LOUIS AGASSIZ FUERTES AWARD

David Lemmon, "Sexual selection and dimorphism in monogamous species: a comparison of two cardueline finches."

STEWART AWARDS

Eric K. Bollinger, "Relationships between hay-cropping and Bobolink (*Dolichonyx oryzivorus*) populations in central New York."
Paul E. Kendra, "Intraspecific brood parasitism in the House Sparrow."
Mark A. Stern, "Site fidelity and mate fidelity in colonial nesting Black Terns."
Cynthia A. Staicer, "The vocal behavior of the Adelaide's Warbler (*Dendroica adelaidae*), an endemic resident on the Island of Puerto Rico."
Tom C. Will, "Dispersal and habitat selection of Blue-winged and Golden-winged warblers in Michigan."
Anne-Marie Wycoff, "The reproductive advantage of territory location in Chestnut-collared Longspurs."

ALEXANDER WILSON PRIZE (for best student paper at the meeting)

Peter Frederick, University of North Carolina–Chapel Hill, "Mating strategies in White Ibis."

FIRST BUSINESS MEETING

The first business meeting was held on 1 June 1984, President Jerome A. Jackson, presiding. He announced the appointment of the Auditing and Wilson Prize committees, and the appointment of new chairmen for the Membership and Student Membership committees. These new chairmen are respectively, Richard Stiehl and Richard N. Conner. Secretary Curtis Adkisson summarized important actions taken by the Council at its meeting: decisions were made on Nice, Fuertes, and Stewart awards, and on Edwards Prizes; Keith Bildstein was elected Editor of *The Wilson Bulletin*; George Hall has been appointed Reviews Editor of the journal.

Robert D. Burns presented the Treasurer's report.

REPORT OF THE TREASURER
1 January 1983 to 31 December 1983

GENERAL FUNDS

RECEIPTS

Dues collected in 1982		
Regular and Sustaining Memberships for 1983	$ 10,663.50	
For 1984	5,888.50	
Family Membership for 1983	222.00	
For 1984	120.00	
Students Memberships for 1983	2,006.00	
For 1984	329.00	
TOTAL DUES		$ 19,229.00

Subscriptions to *The Wilson Bulletin*		
For 1983	$ 7,577.00	
For 1984	4,020.50	
TOTAL SUBSCRIPTIONS		$ 11,597.00
Back issues of *The Wilson Bulletin*		$ 1,092.82
Interest and Dividends		$ 19,703.86
Royalties		$ 605.27
Contributions from Authors		$ 1,774.71
Contributions to the Student Awards Funds		$ 1,251.15
Contributions to Endowment and Life Memberships		$ 2,172.50
TOTAL RECEIPTS—1 Jan.–31 Dec. 1983		$ 57,426.31
DISBURSEMENTS		
The Wilson Bulletin		
December 1982	$ 15,222.12	
March 1983	11,994.39	
June 1983	10,655.03	
September 1983	12,504.16	
Colorplates	1,322.93	
Editorial Assistants and Office Expenses	7,483.46	
TOTAL PRODUCTION COSTS		$ 59,182.09
Additions to Endowment Trust at Central Counties Bank		$ 2,172.50
Deposit of Student Awards Funds to Dreyfus Liquid Assets		$ 1,251.15
Deposit to Awards Funds from Endowment Earnings		$ 2,450.00
1983 Incorporation Fee		$ 5.00
Dues to International Council for Bird Preservation 1983		$ 100.00
Membership Promotions		$ 625.00
Stationery		$ 113.20
Treasurer's Expenses		
Postage, Telephone, and Xeroxing		$ 502.59
Student Membership Mailing		$ 50.00
Refunds		$ 54.00
Ornithological Societies of North America		$ 8,775.03
Treasurer's Bond		$ 51.00
TOTAL DISBURSEMENTS—1 Jan.–31 Dec. 1983		$ 75,331.56
1983 DEFICIT		($17,905.25)

CASH ACCOUNTS

Checking Account, 31 Dec. 1983	$ 6,622.07	
Savings Account, 31 Dec. 1983	201.14	
Dreyfus Liquid Assets, 31 Dec. 1983	33,414.53	
TOTAL CASH ON HAND		$ 40,237.74

DESIGNATED ACCOUNTS

VAN TYNE MEMORIAL LIBRARY FUND

RECEIPTS		
Balance 1982	$ 618.63	
Sales and Gifts	203.75	

DISBURSEMENTS			
Purchase of Books	$	235.15	
Balance of account transferred to Ann Arbor	$	587.43	
BALANCE			$ –0–

Louis Agassiz Fuertes Research Fund

RECEIPTS		
Endowment Earnings	$	600.00
DISBURSEMENTS		
Janice Crook	$	300.00
P. McGill-Harelstad		300.00

Alexander Wilson Prize

RECEIPTS		
Endowment Earnings	$	100.00
DISBURSEMENTS		
Richard and Susan K. Knight	$	100.00

Ernest P. Edwards Prize

RECEIPTS		
Endowment Earnings	$	62.50
E. P. Edwards	$	287.50
DISBURSEMENTS		
Thomas D. Nudds	$	175.00
Charles G. Sibley		87.50
Jon E. Ahlquist		87.50

Paul A. Stewart Awards

RECEIPTS		
Endowment Earnings	$	1,400.00
DISBURSEMENTS		
Opal H. Dakin	$	200.00
Kathryn A. Daniels		200.00
Christopher C. Rimmer		200.00
Bette A. Loiselle		200.00
Timothy C. Lamey		200.00
Jeffrey M. Black		200.00
James G. Devereux		200.00

Aaron Bagg Student Award Fund

RECEIPTS		
Balance from 1982	$	10.00
Endowment Earnings		186.00
DISBURSEMENTS		
14 Student Memberships Awarded	$	196.00

Annual Meeting Reserve Fund

1982 Balance	$	229.00

ENDOWMENT

RECEIPTS

Value of General Endowment Fund, 31 Dec. 1982	$190,008.96	
Life Membership Payments and Gifts	2,172.50	
Appreciation of Principal	6,610.12	
Value of Endowment Fund, 31 Dec. 1983		$198,791.58
Earnings from Endowment for 1982		$ 15,923.17

SECOND BUSINESS MEETING

The second business meeting was convened by President Jackson on Saturday afternoon, 2 June 1984. All proposed new members of the Society were elected unanimously. The Auditing Committee presented its report, which was unanimously approved. The resolutions presented by the Resolutions Committee were approved unanimously.

Nominations Committee Chairman George A. Hall presented the slate of officers for 1984–85: President, Jerome A. Jackson; First Vice-President, Clait E. Braun; Second Vice-President, Mary H. Clench; Secretary, John L. Zimmerman; Treasurer, Robert D. Burns; Elected Member of Council (term to expire in 1987), Jon C. Barlow. There being no further nominations, motion was made, seconded, and passed that instructed the Secretary to cast a unanimous ballot for the slate.

Summaries of selected committee reports to Council are presented below.

AUDITING COMMITTEE REPORT—1983

We, the undersigned, have reviewed and validated the account balances of the Wilson Ornithological Society submitted by the Treasurer for the calendar year ending 31 December 1983. We are satisfied that these records accurately represent the financial transactions for the year and accurately reflect the assets of the Society at year-end.

The Auditing Committee wishes to commend the Treasurer, Dr. Robert D. Burns, for his continued dedication in fulfilling his responsibilities.

William A. Klamm, *Member*
Hubert P. Zernikow, *Member*
Harold Ratcliff, *Member*
Robert A. Whiting, *Member*

EDITOR'S REPORT—1983

In 1983 Volume 95 of *The Wilson Bulletin* contained 740 pages (99 more than Vol. 94), including 36 major articles, 74 notes, as well as book reviews, an index, the annual meeting report, and ornithological news. Volume 95 was the largest Wilson Bulletin ever published.

The editorial staff was the same as reported for 1982, with the addition of Mary C. McKitrick as Index Editor. I thus thank her and the following people for their outstanding efforts on behalf of the Society: Margaret L. May, Associate Editor; Keith L. Bildstein, Gary R. Bortolotti, and Nancy J. Flood, Assistant Editors; Janet T. Mannone and Richard Snell, Senior Editorial Assistants; C. D. Ankney, P. M. Fetterolf, and J. D. Rising, Editorial Assistants; R. J. Raikow, Review Editor; W. A. Lunk, Color Plate Editor; for help in proofreading, M. A. Goldsmith, B. G. Griffin, V. St. Louis, A. Lynch, and A. H. Werden. I wish to acknowledge Mrs. Goldsmith for special clerical help, and Nancy Flood, George Hall, Jerry Jackson, Janet Mannone, and Margaret May for wise counsel and other assistance. With respect to the Bulletin's color plates, a special debt of gratitude is owed to John O'Neill,

who has often provided superb paintings of Neotropical birds or has found someone to do the work in his stead.

The Wilson Bulletin is a special journal with fine traditions and featuring a good blend of research topics. The efforts of many people are required to put together a major international journal. Again, I thank the authors, the reviewers, the WOS executives with whom I have served, the editorial staff of the *Bulletin,* the Royal Ontario Museum, in particular the staff of the Dept. Ornithology (ROM), and the membership of the Society for the cooperation and help so generously provided during my tenure.

Jon C. Barlow, *Editor*

LIBRARY COMMITTEE REPORT—1983

The year seemed to pass more rapidly than usual, and with it another successful year of library activities, with the cooperation of many members and with a lot of hard day-to-day work by Janet Hinshaw. A total of 101 loans, made to 66 members, comprised 340 items, including books, journals, and photocopies where appropriate. Donations came from 37 individuals, among whom A. J. Berger once more must be given outstanding recognition. Special thanks, also, are due George T. Jones, for donating a manuscript, "The Chronicle of Lynds Jones of Oberlin College," which concerns his father, one of the founders of the Society and editor of *The Wilson Bulletin* for 35 years.

Other donors were: R. C. Banks, J. B. Belknap, W. and D. Behling, G. A. Clark, Jr., J. Gapyczynski, G. A. Hall, K. W. Haller, P. Hamel, G. H. Harrison, H. Harrison, J. Hinshaw, S. Holohan, S. Houston, H. Lapham, D. I. MacKenzie, H. Mayfield, P. L. Meininger, W. C. Mullie, Northern Prairie W. R. C., S. Postupalsky, Patuxent W. R. C., J. e. Otto, A. Rea, K.-L. Schuchmann, D. Siegel-Causey, A. Simon, W. Southern, P. A. Stewart, R. W. Storer, W. Thiede, Y. Tsukamoto, J. W. Weber, Col. L. R. Wolfe, M. Wood, and D. Zembal. Their donations included 89 books, 399 reprints and pamphlets, 317 journal issues, 11 monographs and reports, 8 manuscripts, 10 translations, and 1 thesis. Items not needed are offered from time to time for sale or exchange. Thirty-seven new books were purchased; about 700 journal issues were obtained by trade; the sale of duplicates netted $401.50 for the New Book Fund. For 123 exchanges of *The Wilson Bulletin* we received 168 publications; with 29 gifts and 9 regular subscriptions, we received 206 current periodicals, reprints, and books.

We extend our thanks to the entire membership, and urge your continued support.

William A. Lunk, *Chairman*

MEMBERSHIP COMMITTEE REPORT—1983

Total paid membership for the Society was 2880 as of 1 May 1984. Three hundred ninety-seven new members joined the Society this year. My office handled a total of 26 requests for membership applications since the last meeting. Applicants were sent the membership prospectus and a letter asking that dues be sent to OSNA in Ithaca, New York. I encourage anyone interested in using our new display at local meetings to write me.

Keith Bildstein, *Chairman*

STUDENT MEMBERSHIP COMMITTEE REPORT—1983

The availability of Student Membership Awards was announced in *The Wilson Bulletin* and the Ornithological Newsletter, and 205 letters with nomination and application forms were sent to members of the Society in positions to identify eligible students. Application forms were also sent in response to 16 inquiries. Completed applications were received from

22 individuals, of whom 19 qualified for awards. Invitations to join the Society were sent to 16 students. The awardees are: Robin E. Abbey, College of William and Mary; A. Margaret Elowson-Hawley, Univ. Wisconsin; Todd E. Fink, Southern Illinois Univ.; Elizabeth J. Hawfield, Winthrop College; Geoffrey E. Hill, Univ. New Mexico; D. Scott Hopkins, Western Illinois Univ.; Shonah Anne Hunter, Southern Illinois Univ.; Jerry W. Hupp, Colorado State Univ.; Emily D. Kennedy, Rutgers Univ.; Monica G. LeClerc, Brigham Young Univ.; Nancy A. Lutfy, Northern Illinois Univ.; Michael R. North, North Dakota State Univ.; Mark D. Reynolds, Univ. California–Berkeley; Kathryn D. Robinson, Bowling Green State Univ.; Elizabeth I. Rogers, Michigan State Univ.; Greggory J. Transue, Rutgers Univ.

John L. Zimmerman, *Chairman*

REPORT OF THE RESOLUTIONS COMMITTEE

WHEREAS, The Wilson Ornithological Society has for many years benefitted by the active participation in both its scientific program and its business affairs by scientists of the U.S. departments of the Interior and Agriculture, who serve or have served as officers, council members, editors, and chairmen and members of important committees, and

WHEREAS, official participation of these scientists has been severely curtailed because of lack of administrative support and funding, and by an official policy of discouraging such participation as of lowest travel priority, and

WHEREAS, communication with government scientists at meetings provides a means of input from the scientific community to federal research and management policies, and

WHEREAS, meetings of professional and scientific societies promote an interchange of ideas that increases the quality of research and stimulates new approaches to solving problems, thus promoting greater efficiency in federal programs, and

WHEREAS, exchanges at meetings often lead to vastly increased cooperation between the private and public sectors of the research community that, in turn, can result in the avoidance of repetition, competition, and redundancy of effort by different parts of the research community, and

WHEREAS, the curtailment of attendance of U.S. Government scientists at meetings of professional scientific societies will ultimately result in the impoverishment of the quality and quantity of research and management accomplished by the federal government,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society urges the departments of the Interior and Agriculture to assign a higher priority to scientific meeting attendance, and permit and encourage attendance at such meetings by their scientists.

WHEREAS, the proposed Emergency Wetlands Resources Act before Congress (S. 1329, H.R. 3082) is designed to increase federal funding to acquire wetlands, and

WHEREAS, preservation of natural areas rescues wildlife from the threat of extinction, thus providing natural beauty and saving species which, in time, may prove to benefit humankind in the form of new crops, new medicines, etc., and

WHEREAS, these wetlands, among the richest and most productive of habitats, are under severe pressure to be drained for agriculture, building and other development, and

WHEREAS, a rider, Title IV, has been attached to H.R. 3082 transferring National Park and Wildlife Refuge land in North Carolina to the Corps of Engineers so that they can build mile-long stone jetties on either side of Oregon Inlet on the Outer Banks, and

WHEREAS, the proposed jetties constitute an experiment that is economically unjustified and, potentially, can have devastating effects on wildlife, recreation, commerce, and tourism in coastal North Carolina,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society strongly urges the respective Houses of Congress to support and pass the Emergency Wetlands Act, and, at

the same time, the Society urges the House to repeal the rider Title IV, attached to the Act, H.R. 3082.

WHEREAS, the preservation of the nation's wetlands is widely recognized as one of the needs most critical to maintaining viable populations of waterfowl, waders, and shorebirds, as well as the populations of many other species of birds, mammals, and other wildlife, and

WHEREAS, wetlands are being destroyed nationwide at an increasingly rapid pace, and

WHEREAS, nearly 120,000 acres of prime wetlands and forest lands in Dare and Tyrell counties of North Carolina, valued at more than $50 million, will now be preserved as a part of the National Wildlife Refuge System as a result of the generosity of The Prudential Insurance Company of America, and

WHEREAS, The Nature Conservancy, recognizing that this area is important to migratory waterfowl, constitutes excellent wildlife habitat, and is the northernmost limit of the American alligator, has been working with The Prudential since 1980 in an effort to secure the land as a natural wildlife area, and

WHEREAS, this is an outstanding example of effective cooperation between industry, government, and a private conservation organization leading to the preservation of a major natural resource for the ultimate benefit of the environment, of wildlife, and of the general public,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its appreciation to The Prudential Insurance Company of America, to The Nature Conservancy, and to all individuals involved in the establishment of the Alligator River National Wildlife Refuge in North Carolina's Pamlico-Albermarle Peninsula.

WHEREAS, Curtis S. Adkisson has served The Wilson Ornithological Society for six years in the vital communicating link of Secretary, and

WHEREAS, he has executed his duties with an unfailing combination of efficiency and good humor,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its gratitude to Curtis S. Adkisson for his service to the Society.

WHEREAS, Jon C. Barlow has served as Editor for six volumes of *The Wilson Bulletin,* and

WHEREAS, he has maintained a consistently high level of scholarship, especially in the face of difficult financial times, and

WHEREAS, under his editorship the largest volume ever of *The Wilson Bulletin* (1983) has been published,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its gratitude to Jon C. Barlow for his service to the Society.

WHEREAS, Robert J. Raikow has served The Wilson Ornithological Society for the exceptional term of 10 years as Review Editor of *The Wilson Bulletin,* and

WHEREAS, the growth in ornithological literature has made this position one of increased responsibility, and

WHEREAS, during Dr. Raikow's editorship a consistently high quality of critical scholarship has been maintained in *The Wilson Bulletin*'s review section,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its gratitude to Robert J. Raikow for his service to the Society.

WHEREAS, The Wilson Ornithological Society has held its 65th Annual Meeting in Wilmington, North Carolina, 31 May–2 June 1984, at the invitation of the University of North Carolina at Wilmington and the Cape Fear Bird Club, and in conjunction with the spring meeting of the Carolina Bird Club, and

WHEREAS, the natural splendor of coastal North Carolina was coupled with southern hospitality as manifested by that unique endemic species, the Shrimp-a-roo, and

WHEREAS, the flawless progression of all aspects of the meeting can be attributed to the hard work and meticulous attention to details by a devoted local committee,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its appreciation and gratitude to James F. Parnell and his Local Committee on Arrangements, to the Cape Fear Bird Club, to Mary H. Clench who organized the scientific program, and to the staff of the University of North Carolina at Wilmington who helped to make our visit to Wilmington a productive and memorable meeting.

PAPERS SESSION

The scientific papers session was arranged by Mary H. Clench. Individual sessions were chaired by Curtis Adkisson, Clait Braun, Mary Clench, Abbot Gaunt, George Hall, Jerome Jackson, Helen Lapham, Kenneth Parkes, and Richard Stiehl.

Sidney A. Gauthreaux, Jr., Clemson University, Clemson, SC 29631, "Radar measurements of the altitude of trans-Gulf migration."

David M. Mark, SUNY at Buffalo, Buffalo, NY 14260, "North–south 'mirror-image' navigational error in migrating birds: the Fork-tailed Flycatcher in North America."

Thomas A. Waite and Thomas C. Grubb, Jr., The Ohio State University, Columbus, OH 43210, "Diet selection within a captive bark-foraging guild during winter."

Stephen A. Nesbitt, Florida Game and Fresh Water Fish Commission, Gainesville, FL 32601, "Pair formation and fidelity in Sandhill Cranes."

Richard W. Knapton, Brock University, St. Catharines, Ont. L2S 31A, "A comparison of male and female contributions to feeding nestlings in the Nashville Warbler."

Douglas A. Gross, Ichthyological Associates, Inc., Berwick, PA 18603, "Residential status and occurrence of helpers at the nest of Blue Jays (*Cyanocitta cristata*) in Pennsylvania."

Bill Hilton, Jr., University of Minnesota, Minneapolis, MN 55455, "Breeding strategy and fledgling dispersal in Blue Jays (*Cyanocitta cristata*)."

Peter Frederick, University of North Carolina, Chapel Hill, NC 27514, "Mating strategies in White Ibis."

John W. Chardine, Brock University, St. Catharines, Ont. L2S 3A1, "Adaptive significance of copulation disruption in the kittiwake based on observations of marked individuals."

William C. Alexander, Georgia Southern College, Statesboro, GA 30460, "A comparison of intersexual aggression in nonbreeding diving ducks (Aythyini)."

Anna E. Ross, Clemson University, Clemson, SC 29631, "Behavioral dominance in White-crowned Sparrows (*Zonotrichia l. leucophrys*)."

Stephen J. Wagner, Clemson University, Clemson, SC 29631, "Intraspecific dominance hierarchies among Song and White-throated sparrows."

V. M. Case, Davidson College, Davidson, NC 28036, "Breeding cycle aggression in two colonies of Zebra Finches."

J. D. Rising, University of Toronto, Toronto, Ont. M5S 1A1, "Review of sexual size dimorphism in American passerine birds."

G. Thomas Bancroft, University of South Florida, Tampa, FL 33620, "Growth and sexual dimorphism of the Boat-tailed Grackle."

Gilbert S. Grant, North Carolina State Museum, Raleigh, NC 27611, "Microclimate of Gull-billed Tern and Black Skimmer nests."

John L. Zimmerman, Kansas State University, Manhattan, KS 66506, "Comparative water consumption in *Spiza* and *Calamospiza*."

Marcus D. Webster, Franklin College, Franklin, IN 46131, "Water and heat loss through avian integuments: the role of the plumage."

Sharon F. Simpson, Ohio University, Athens, OH 45701, "The shoulder region of the House Sparrow."

Robert W. Repenning and Ronald F. Labisky, Florida Cooperative Fish and Wildlife Research Unit, Gainesville, FL 32611, "Effects of even-age timber management on the breeding bird community of longleaf pine flatwoods."

David S. Lee and Eloise F. Potter, North Carolina State Museum, Raleigh, NC 27611, "Quantifying breeding birds associated with pocosins: an exercise in community definition and myth slaying."

George A. Hall, West Virginia University, Morgantown, WV 26506, "A long-term bird population study in an Appalachian spruce forest."

Trevor L. Lloyd-Evans and R. Brent Bailey, Manomet Bird Observatory, Manomet, MA 02345, "Census methods in dense eastern woodland."

James F. Parnell, Mark A. Shields, UNC–Wilmington, NC 28403, and Donald A. McCrimmon, Cornell University, Ithaca, NY 14850, "Trends in nesting populations of colonial waterbirds in North Carolina estuaries."

Robert G. Hooper, USDA Forest Service, Charleston, SC 29407, "Red-cockaded Woodpecker response to cavity tree removal."

Richard R. Repasky and Phillip D. Doerr, North Carolina State University, Raleigh, NC 27695, "Substrate utilization by foraging Red-cockaded Woodpeckers."

R. D. Teitelbaum and W. P. Smith, Southeast Louisiana University, Hammond, LA 70402, "Cavity-site characteristics of the Red-cockaded Woodpecker in Fountainebleau State Park, Louisiana."

Richard N. Conner, Kathleen A. O'Halloran, and J. Howard Williamson, USDA Forest Service, Nacogdoches, TX 75962, "Status of Red-cockaded Woodpecker colonies on the Angelina National Forest, Texas."

Curtis S. Adkisson, VPI&SU, Blacksburg, VA 24061, "Vocal differentiation and behavior in Scandinavian crossbills."

Gary Ritchison, Eastern Kentucky University, Richmond, KY 40475, "The responses of cardinals to the songs of male and female conspecifics."

Cheryl A. Logan, University of North Carolina, Greensboro, NC 27412, "Fall territorial dynamics in mockingbirds."

T. David Pitts, University of Tennessee, Martin, TN 38328, "Reduced nesting success of Carolina Chickadees during abnormally wet and cool weather."

John M. Hagan, III, North Carolina State University, Raleigh, NC 27695, "Collecting time-budget data on Ospreys using a microcomputer."

Richard C. Banks, National Museum of Natural History, Washington, DC 20560, "Everything you've always wanted in a Greater Scaup, and Lesser."

Helmut C. Mueller, University of North Carolina, Chapel Hill, 27514, "Some differences between owls and hawks."

Nicolaas A. M. Verbeek, Simon Fraser University, Burnaby, BC V5E 2T4, "Behavioral interactions between accipiters and their avian 'prey'."

J. E. Cely and J. A. Sorrow, Jr., South Carolina Wildlife and Marine Resources Department, Columbia, SC 29202, "American Swallow-tailed Kite home range and habitat utilization in South Carolina."

James H. Mathis, Northwestern High School, Rock Hill, SC 29730, "Feeding habits of Black Vultures (*Coragyps atratus*)."

Julie A. Hovis, Wilmington, NC 28405, and William G. Mattox, Greenland Peregrine Falcon

Survey, Columbus, OH 43229, "Behavior of Peregrine Falcons at a nest in west Greenland."

David G. Jennings, University of Georgia, Athens, GA 30602, "An efficient raptor trap for sampling over large areas."

ATTENDANCE

COLORADO: *Fort Collins,* Clait Braun.

DELAWARE: *Greenville,* David Niles.

FLORIDA: *Gainesville,* Mary Clench, Robert Repenning; *Lehigh Acres,* Ben Kiff, Maxine Kiff; *Maitland,* Herbert Kale; *Tampa,* Ann Bancroft, Tom Bancroft.

GEORGIA: *Atlanta,* Didi Manns, Robert Manns; *Augusta,* Emil Urban, Mrs. Louis Urban; *Statesboro,* William Alexander, Bill Lovejoy, Mrs. Bill Lovejoy.

ILLINOIS: *Colchester,* Edwin Franks, Evelyn Franks; *Dennison,* Peter Stacey; *Grays Lake,* Scott Hickman.

INDIANA: *Franklin,* Marcus Webster.

KANSAS: *Manhattan,* John Zimmerman.

KENTUCKY: *Richmond,* Gary Ritchison, Mrs. Gary Ritchison.

LOUISIANA: *Baton Rouge,* Douglas Pratt; *Metairie,* Cecil Kersting; *Hammond,* Winston Smith.

MARYLAND: *Baltimore,* Janet Gailey-Phipps; *Columbia,* Sallie Simpson.

MASSACHUSETTS: *Manomet,* Linda Leddy, Trevor Lloyd-Evans; *Wellesley Hills,* Sally McNair.

MICHIGAN: *Ann Arbor,* Janet Hinshaw, Stephen Hinshaw; *Grass Lake,* Harold Ratcliff; *Jackson,* Robert Whiting; *Pleasant Lake,* Hubert Zernichow.

MISSISSIPPI: *Mississippi State,* Opal Dakin, Bette Jackson, Jerome Jackson.

NEW JERSEY: *Lyndhurst,* Douglas Kibbe; *Pitman,* Andrea Roth; *Somerset,* Bertram Murray, Patti Murray; *Trenton,* Mary Doscher.

NEW MEXICO: *Albuquerque,* David Ligon.

NEW YORK: *Ithaca,* Charles Walcott; *Lansing,* Elise Lapham, Helen Lapham; *Tonawanda,* David Mark.

NORTH CAROLINA: *Aberdeen,* Evelyn Stalnaker, Harold Stalnaker; *Arden,* Marcia Perdue; *Bat Cave,* Ron Warner; *Carolina Beach,* Jane Brackett; *Chapel Hill,* Peter Frederick, Helmut Mueller, Nancy Mueller; *Charlotte,* William Brokaw, Daphine Doster, Bill Cobey, Flo Cobey; *Davidson,* Verna Case; *Durham,* A. A. McCoy, Marcus Simpson, Melinda Welton; *Fairview,* Jerry Young, Ruth Young; *Fayetteville,* Phillip Crutchfield; *Graham,* Lynn Moseley; *Greensboro,* Dot Garrett, H. Hendrickson; *Pinehurst,* Bonnie Israel; *Pisgah Forest,* Bill Hough, Jean Hough; *Pleasant Garden,* Cheryl Logan; *Raleigh,* Alice Allen-Grimes, Paul Curtis, Phil Doerr, Paula Ford, Gilbert Grant, John Hagan, Fran Irvin, Wayne Irvin, David Lee, Thomas Quay, Dick Repasky, Jeffery Walters; *Reidsville,* Bob Maus; *Sea Grove,* Bolenda Ferree; *Wilmington,* Robin Bjork, John Brunjes, Richard Dillaman, Dargan Frierson, Bill Hofmann, Julie Hovis, Lee Jackson, Mrs. Frank Kosh, Greg Massey, Jeremy Nance, James Parnell, Mrs. James Parnell, Betty Rullman, Jennifer Slack; *Winston-Salem,* George Morgan, Mrs. George Morgan; *Wrightsville Beach,* Frances Needham; *Zebulon,* Eloise Potter.

OHIO: *Athens,* Sharon Simpson; *Columbus,* Abbot Gaunt, Sandra Gaunt, Thomas Grubb, Jr., Thomas Waite; *Gambier,* Robert Burns; *Lakewood,* William Klamm, Nancy Klamm; *Painesville,* Carl Newhous, Mary Newhous; *University Heights,* Bruce McLean.

PENNSYLVANIA: *Clarks Summit,* Michael Carye; *Orangeville,* Douglas Gross, Cindy Hose; *Pittsburgh,* Kenneth Parkes.

SOUTH CAROLINA: *Aiken,* Jeannine Angerman; *Charleston,* Dennis Forsythe, Robert Hooper,

William Post; *Chester,* Mary Robinson, Mrs. W. C. Stone, Sr.; *Clemson,* Sidney Gauthreaux, Anna Ross, Steven Wagner; *Columbia,* John Cely, Susan Gawarecki, Stephen Perry; *Lodson,* Dave Harvey; *Myrtle Beach,* Margaret Wren; *Rock Hill,* Keith Bildstein, Bill Hilton, James Mathis, Neville Yoon; *Six Mile,* Douglas McNair; *Spartanburg,* Miller Foster, Jr., Mrs. Miller Foster, Jr.; *Summerville,* Jean Wattley.

TENNESSEE: *Knoxville,* Marcia Davis, Beth Lacy; *Martin,* David Pitts; *Maryville,* Ralph Zaenglein; *Memphis,* George Payne, Jr.; *Norris,* Charles Nicholson.

TEXAS: *Nacogdoches,* Richard Conner.

VIRGINIA: *Alexandria,* Richard Banks, Beth Ann Sabo; *Blacksburg,* Curtis Adkisson, Karen Adkisson; *Manassas,* Roxie Laybourne; *Sweet Briar,* Ernest P. Edwards; *Williamsburg,* Mitchell Byrd, Chuck Rosenburg, David Wallin.

WEST VIRGINIA: *Bethany,* Albert Buckelew, Jr.; *Elkins,* Eugene Hutton; *Morgantown,* George Hall.

WISCONSIN: *Green Bay,* Sherry Sanderson, Richard Stiehl.

BRITISH COLUMBIA: *Burnaby,* Nico Verbeek.

ONTARIO: *Gores Landing,* Norma Martin, Norman Martin; *St. Catharines,* John Chardine, Richard Knapton; *Toronto,* Jon Barlow, Deron Barlow, Brete Griffin, Janet Mannone, Margaret May, Thomas Parsons, James Rising.

NEW BRUNSWICK: *Sackville,* Anthony Erskine, Janet Erskine.

ADDRESS UNAVAILABLE: Bob Bryand, Doug Davis, Timothy Deline, Bill Faust, Katy Hick, Chris Kellner, John Smallwood.

1985 ANNUAL MEETING

The Sixty-sixth Annual Meeting of The Wilson Ornithological Society will be held jointly with The Cooper Ornithological Society meeting, at the Unviersity of Colorado, Boulder, Colorado, 6–9 June 1985. Cynthia Carey is chairing the Local Arrangements Committee. Her address is: Dept. EPO Biology, Univ. Colorado, Boulder, CO 80309.

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By Mary C. McKitrick

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